# Seasonal Activity Patterns of Bats in the Central Appalachians

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*Abstract*

Two threats to bats are especially pervasive in the central Appalachian Mountains of the eastern United States: White-nose Syndrome (WNS) and wind energy development. These threats are sufficient that multiple species are at risk of regional extirpation. White-nose Syndrome has caused the death of millions of bats in North America, and multiple hibernating bat species are affected in the central Appalachians (Indiana bat, *Myotis sodalis*; northern long-eared bat, *Myotis septentrionalis*; little brown bat, *Myotis lucifugus*; eastern small-footed bat, *Myotis leibii;* eastern tricolored bat, *Perimyotis subflavus;* big brown bat, *Eptesicus fuscus*). Population declines attributed to WNS have led to the listing the northern long-eared bat as threatened under the Endangered Species Act, and other affected bat species are likely to follow. Wind energy is one of the most rapidly-growing energy sources in eastern United States, and primarily affects highly migratory, non-hibernating bat species in the Appalachians (eastern red bat, *Lasiurus borealis*; silver-haired bat, *Lasionycteris noctivagans*; hoary bat, *Lasiurus cinereus*). This anthropogenic threat could cause the collapse of migratory bat populations, especially if operational mitigation strategies are not implemented moving forward in the future especially as more wind energy production facilities are installed. These threats represent great challenges for land managers to reduce additional potential impacts to bats from other stressors such as other management actions, i.e., forest management, prescribed fire, and urbanization/habitat conversion. Baseline data is neededto help inform management decisions relative to bats. However, managers in the Appalachians have limited data on general and species-specific activity and distributional patterns, especially during the spring and autumn seasons; necessary information for formulating suitable management strategies to benefit bat conservation. Furthermore, the effects of these primary threats to populations of hibernating and migratory bat species may be exacerbated

during autumn and spring. Wind energy and WNS affect individual bat species differently, and the extent of impacts can vary seasonally. Therefore, I sought to determine patterns and drivers of activity for hibernating bat species during autumn and spring around hibernacula. Similarly, I set out to determine patterns and drivers of activity for migratory bat species during autumn and spring along ridgelines in the central Appalachians. I also explored data to search for potential WNS-induced changes to summer ecology of northern long-eared bats, a species once common in the central Appalachians. This study can help elucidate patterns of bat activity during largely understudied seasons. Furthermore, it can provide useful information needed by land managers to implement actions that could help alleviate and/or avoid potential additive negative impacts on bat species with existing conservation concerns.

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***Abstract***

Bat conservation and research efforts largely have focused on summer maternity colonies and winter hibernacula, leaving immediately pre- and post-hibernation ecology for most species unclear. Understanding these topics is critical for addressing potential additive impacts to White-nose Syndrome (WNS)-affected bats, especially during staging for hibernation and migration, respectively. To examine fall and spring bat activity patterns in the Appalachian Mountains of Virginia and West Virginia, we acoustically monitored bat activity around three hibernacula from early September through mid-November 2015 and 2016, and from early March through April 2016 and 2017. We assessed the effects of distance to hibernacula and ambient conditions on nightly bat activity using generalized linear mixed effects models. Overall bat activity was extremely limited at all sample sites through both the fall and spring sample periods except at sites proximal to hibernacula entrances. Best-supported models describing bat activity varied amongst individual bat species and species-groups, but date and ambient temperatures generally appeared to be major drivers of activity in autumn and spring. Overall, autumn bat activity around hibernacula was variable through the sampling period, but total activity for all species had largely ceased by mid-November. Spring bat activity also varied through the sampling period, and bats were active by mid-March.

*Introduction*

      Prior to hibernation, many temperate biome cave bat species "swarm" around hibernacula to mate and find suitable hibernation sites (Davis and Hitchcock 1965, Barclay et al. 1979, Schaik et al. 2015). This time also is vital for weight gain and fat deposition, a necessity to survive the energy demands of hibernation (Ewing et al. 1970, Kunz et al. 1998, Jonasson and Willis 2011, Reeder et al. 2012). White-nose Syndrome (WNS) has caused millions of bats to die during hibernation, largely due to changes in behavior that deplete energy reserves (Blehert et al. 2009, Frick et al. 2016). During the late summer and early fall, hundreds of individual bats may engage in swarming behavior outside a hibernaculum (Rivers et al. 2005, Schaik et al. 2015), with males being most active (in flight more hours each night) and for a longer period into the autumn at or near hibernacula (Schowalter 1980, Lowe 2012, Burns and Broders 2015). Prior to entering hibernation in mid- to late-fall, bats continue to roost on the landscape, in trees, rocks, and human structures (Brack 2006, Lowe 2012). Effects of ambient conditions on bat activity, regardless of sex, during the fall swarming period, and specifically around known hibernacula, are understood poorly. A greater examination of how ambient conditions affect the timing of fall swarm activity and subsequent hibernation phenology could help managers actively define and manage critical autumn swarm habitat. These insight may help prevent accidental 'take', as defined under Section 3 of the Endangered Species Act (ESA 1973, as amended; U.S. Office of the Federal Register 2015), especially with regard to the federally-endangered Indiana bat (*Myotis sodalis;* hereafter MYSO).

      During the spring emergence/staging period, cave hibernating bats emerge from caves and disperse across the landscape, with reproductively-active females establishing maternity

colonies (Caire et al. 1979, Whitaker and Hamilton 1998). Emerging bats typically do not re-enter hibernacula, instead roost across the landscape. However, observations of spring roost sites are limited compared to well-studied summer roosts (Britzke et al. 2006). Foraging and prey availability around hibernacula during the spring, when energy demands are high post-hibernation, are important factors affecting movement to maternity areas and subsequent reproductive success (Frick et al. 2016, Meyer et al. 2016). Though spring emergence may not be triggered by prey availability *per se,* and is probably linked directly to temperature and pressure changes, photoperiod, and circannual rhythms. Meyer et al. (2016) suggested that female bats' arrival at colony areas coincides with increasing insect abundance, even if prey availability was low at first emergence.

Migration to maternity areas consumes valuable energy stores, and WNS-related impairments could exacerbate energy losses in impacted species (Britzke et al. 2006, Frick et al. 2016). There appear to exist considerable differences in spring ecology between populations and geographic regions. For example, female MYSO in the midwestern United States may travel as far as 100-500 km to reach summer maternity areas, whereas female MYSO from hibernacula in New York travelled only 27 km, on average (Kurta and Murray 2002, Britzke et al. 2006, Pettit and O'Keefe 2017). Data about spring movements are lacking for northern long-eared bats (*Myotis septentrionalis*; hereafter MYSE), and while not typically considered a 'migratory' bat species, they can travel up to 160 km to summer foraging/maternity colony areas (USFWS, 2014). Because these migrations pose great energy demands, foraging may be an important activity immediately post-emergence. Foraging success, however, is tied closely to prey availability, which in turn is affected by weather conditions (Williams 1940, Meyer et al. 2016). Spatio-temporal assessments of bat activity post-emergence will allow managers to recognize

vital habitat and time periods, thus encouraging management that provides maximum conservation benefit to dwindling bat populations in the central Appalachians. Accordingly, the dynamics of bat activity during autumn swarm and spring staging seasons, both immediately around hibernacula and elsewhere are critical data gaps for post-WNS species management.

Critical to understanding the effects of WNS on emergence timing and dynamics (Blehert et al. 2009, Frick et al. 2016) is the influence on reproductive output (Czenze and Willis 2015). Female bats emerge earlier than males regardless of WNS-related impacts (Norquay and Willis 2014, Czenze and Willis 2015), and WNS causes bats (regardless of sex) to emerge earlier in the spring (Blehert et al. 2009, Norquay and Willis 2014), which may prove detrimental to species recruitment. Clearly, WNS compromises female bats' physiologic conditions during hibernation (Frick et al. 2016). To this effect, Francl et al. (2012) proposed that female bats may abort pregnancy if crucial energy sources are too limited to provide ample energy required for fetal or juvenile development.

In other mammalian taxa (e.g., genus *Marmota*), reproductive success is greater with earlier emergence from hibernation in favorable conditions (Ozgul et al. 2010), but this remains speculative for bats (Czenze and Willis 2015). Unlike larger mammals, bats may not be able to withstand the danger of a cold snap in the early spring. Furthermore, WNS increases overwinter energy consumption, and reproductive failure may negate any physiological benefits of emerging earlier. Females lacking the physiological energy constraints of pregnancy may have fewer behavioral/roosting constraints, thus could conceivably emerge from hibernation very early with less deleteriouseffects, though this remains speculative. Non-reproductive females may have a better chance of surviving through the spring and summer.

Under the Indiana Bat Protection and Enhancement Plan Guidelines (USFWS 2009), hibernacula where MYSO exist are afforded protective buffer zones, where tree clearing activities are seasonally restricted. Within an 8 km radius of Priority 3 and Priority 4 MYSO hibernacula (USFWS 2007), tree clearing must occur between November 15 and March 31 to avoid disturbing MYSO day-roosting in trees (USFWS 2009). These guidelines aim to minimize adverse effects on Indiana bats during the fall swarm and spring emergence periods when they use forested habitats surrounding hibernacula.

A regional understanding of acoustic bat activity patterns around hibernacula during spring and autumn will help determine the sufficiency of these protective cave buffers, especially for the federally-listed species such as MYSE and MYSO whose populations have declined substantially due to WNS. Broadly, acoustic bat activity can be defined as a count of echolocation pass files (hereafter activity). In Virginia, Powers et al. (2015) found evidence of massive WNS-induced population declines across multiple bat species; yet whether population declines and physiologic changes affect spring and autumn activity remains unclear.

My objectives were to determine major activity patterns and define drivers of activity of cave-hibernating bats during the pre-hibernation staging period and the spring emergence period around caves in the central Appalachians after the onset of WNS. I hypothesized that activity would greatly vary both temporally and spatially around caves, but activity would occur throughout the sampling season, specifically proximal to cave entrances (Whitaker and Rissler 1992, Bernard and McCracken 2017). Furthermore, I hypothesized that ambient conditions act as indicators and cause bats to restrict or increase activity during autumn and spring in habitats around caves.

*Methods*

*Study Area*

I conducted my study around two caves in the Virginia Ridge and Valley sub-province of the Appalachian Mountains and one cave in the West Virginia unglaciated Appalachian Plateau sub-province (Figure 1-1). These three caves were chosen because of similar numbers of hibernating Indiana bats pre-WNS along with multi-year cave-count records (Powers et al. 2015), and a south to north clinal arrangement pattern on the regional landscapes. Each of the three caves sampled are considered Priority 3 hibernacula (based on cave count data, USFWS 2007). The two Virginia caves I studied are located in Bath and Bland counties (hereafter Caves A and B, respectively), and the West Virginia cave is located in Tucker County (hereafter Cave C; specific names withheld to protect locations of federally-listed species' hibernacula; U.S. FCRPA 1988). The forests surrounding Caves A and B are generally xeric-to moderately mesic oak (*Quercus* spp.) associations on ridges and other areas with well-drained soils, and mixed mesophytic forest along riparian areas and north-facing aspects (Braun 1950). The predominant forest surrounding Cave C is a mixed mesophytic/Allegheny hardwood association (Ford et al. 2005). The landscape immediately surrounding both Cave A and Cave C is primarily forested, whereas the landscape surrounding Cave B is a matrix of forest and agricultural land.

*Data Collection*

In the autumn, I monitored bat activity at the main entrance of each cave and at one km, two km, and three km distances from cave entrances (Figure 1-2) from early September to mid-November in 2015 and 2016, when cave bats swarm and mate around hibernacula. For the spring, I monitored bat activity in early March to late April in 2016 and 2017, when bats are leaving hibernacula and dispersing across the landscape for the summer months (Whitaker and

Rissler 1992, Caceres and Barclay 2000). For each cave, only one detector was placed near the cave entrance (away from acoustically reflective surface), and two were deployed at each radii distance. Detector locations were chosen based on accessibility (landowner permission and topography), likelihood of MYSE and MYSO presence (Ford et al. 2005), and site characteristics known to produce high-quality call recordings (i.e., low clutter such as a forest canopy gap/riparian corridor). Detectors at the same radii were spaced > 100 m apart to ensure that individual bats were not sampled on two detectors simultaneously and to maintain quasi-independent sampling units (Ford et al. 2005). I recorded acoustic data using Song Meter ZC detectors (SMM-U1 microphones), Song Meter SM2 (SMX-U1 microphones), and Song Meter SM4 detectors (SMM-U1 microphones, Wildlife Acoustics, Maynard, Massachusetts). I programmed detectors to record nightly from 1900 to 0700 hours. I collected local weather data in Meteorological Terminal Aviation Routine (METAR) format from digital records, from the airport nearest to each detector site (https://www.wunderground.com/, 2017).

I identified acoustic call data to species using the United States Fish and Wildlife Service approved Kaleidoscope version 4.3.1 (Wildlife Acoustics, Maynard, Massachusetts) classifier 4.2.0 at the neutral setting, with default signal parameters (8-120 KHz frequency range, 500 maximum inter-syllable gap, minimum of two pulses, enhance with advanced signal processing (USFWS 2017*a*). I manually checked recorded files using program Analook (Titley Electronics, Columbia, Missouri) to ensure there were no major misclassification errors (e.g., noise files consistently classified as bat echolocation pass). I was not concerned with overall accuracy of the program to assess levels of activity, as all bat species examined were known to be present at my sites, therefore I assumed constant bias in automated file identification (Ford 2017).

*Statistical Analyses*

I created a set of *a priori* candidate models representing specific hypotheses about the relationship between habitat variables and bat activity, using the variables and models for analyses of both fall and spring data. Candidate models included combinations of date, site, landscape characteristics, and ambient conditions (**Error! Reference source not found.**, Table 1-2). I assessed multicollinearity among predictors to ensure highly correlated variables were not included within the same model using package corrplot (Wei and Simko 2016) in program R version 3.2.3 (R Core Team 2013). I tested for autocorrelation in daily bat activity, for each species using R package nlme (Pinheiro et al. 2017). I modelled nightly acoustic bat activity using negative binomial mixed models (GLMM), with nested random effects to account for the correlated nature of sites around caves and repeated measures at sites. I fit negative binomial mixed models using R package glmmADMB (Fournier et al. 2012). I used negative binomial mixed models because bat activity data are counts, and variance was greater than the mean. Because I expected nonlinear changes in bat activity over the sampling period, I compared fully parameterized models with different polynomial structures on date for each species and species group. I used a two-step information theoretic approach; first ranking models with polynomial structures on date using Akaike's Information Criterion corrected for small sample size ($AIC_c$ from package MuMIn; Bartoń 2015; Burnham and Anderson 2002), then using the best-supported polynomial structure for all subsequent candidate models representing *a priori* hypotheses. If models were competing ($\Delta AIC_c < 2$) I used the model with the lowest polynomial order, to avoid overfitting. I centered and scaled all continuous predictors to allow me to assess main effects of interactions (Schielzeth 2010).

I included a set of models for all *Myotis* bat species grouped together (hereafter *Myotis* spp.), and all cave-dwelling bat species grouped together (*Myotis* spp. with PESU and EPFU, hereafter 'cavebats'). The 'cavebats' grouping was analyzed because all cave-dwelling species in my study range are impacted by WNS, and I sought to identify drivers of general bat activity in autumn and spring (Frick et al. 2016). Similarly, I analyzed thee *Myotis* spp. because all *Myotis* species are the genus most heavily impacted by WNS, and to assess activity with less possible bias from species misclassification associated with automated identification software for the genus. I also ran models for MYSO, MYSE, and EPFU individually because I expected differences in activity patterns among species. For example, EPFU represent a cave-dwelling species with rather different life history than most *Myotis* spp; notably EPFU are impacted less by WNS and, in the southern United States, tend to prefer human structures for roost sites (Kunz 2013, Frank et al. 2014). I compared competing hypotheses using $AIC_c$ (Burnham and Anderson 2002). Two cave-dwelling species, MYLE and PESU, were excluded from the individual species analysis due to limited data. Little brown bats were excluded because hibernating population numbers are and were historically very different between sampled hibernacula (R. Reynolds, Virginia Department of Game and Inland Fisheries, pers. comm., Powers et al. 2015). To test for the existence of interacting effects of date and distance to hibernacula on bat activity, I fit *post hoc* models for each species/group for both autumn and spring.

### Results

I acoustically sampled 22 sites around three caves, in autumn 2015, spring 2016, autumn 2016, and spring 2017. I sampled for 68 and 97 nights over autumn 2015 and 2016, and for 49 and 56 nights during spring 2016 and 2017, respectively. Though my objective was to sample

continuously across each season, due to detector failure, and inaccessibility due to weather, some

detector sites were not sampled continuously. I limited analyses to include only call data with a

minimum of three call pulses, to help optimize sensitivity and specificity.

*Autumn activity patterns*

My best supported model describing *Myotis* spp. activity received 88 percent of the

overall model support and contained the following variables: date, a 2$^{nd}$ order polynomial term

on date, year, mean daily temperature, change in mean daily temperature, mean daily wind

speed, change in mean daily wind speed, change in binary precipitation, distance to cave, and an

interaction between date and mean daily temperature (Table 1-3). No other models were

competing. Among continuous predictors, date and mean daily temperature had the largest effect

sizes (Table 1-3). *Myotis* spp. activity was substantially greater proximal to cave entrances

relative to distal sites (Table 1-3), and decreased over the season. However, both were related

positively to mean daily temperature. Temperature and date interacted, such that temperature had

a stronger impact on activity later in the season (Figure 1-3). Although contained in the best

supported model, change in mean daily temperature, mean daily wind speed, change in mean

daily wind speed, and change in binary precipitation had minimal effect sizes (Table 1-3).

Overall *Myotis* spp. activity was lower in 2016 than 2015 (Figure 1-3). *Post-hoc* modelling

indicated that there was no substantial interaction between date and distance to hibernacula

(Table 1-4).

The best supported model describing 'cavebat' activity contained the following variables:

date, a 2$^{nd}$ order polynomial term on date, year, mean daily temperature, change in mean daily

temperature, mean daily wind speed, change in mean daily wind speed, change in binary

precipitation, distance to cave, and an interaction between date and mean daily temperature

(Table 1-5). Among those, date, mean daily temperature, and distance to cave had the largest effect sizes (Table 1-5). 'Cavebat' activity was substantially greater proximal to cave entrances relative to distal sites, and decreased over the season, but both were related positively to mean daily temperature. Temperature and date interacted, such that temperature had a stronger impact on activity later in the season (Figure 1-4). Although contained in the best supported model, change in mean daily temperature, mean daily wind speed, change in mean daily wind speed, and change in binary precipitation had minimal effect sizes (Table 1-5). 'Cavebat' activity was marginally lower in 2016 than 2015. *Post-hoc* modelling indicated that there was no substantial interaction between date and distance to hibernacula (Table 1-6).

The best supported model describing EPFU activity contained the following variables: date and its 4$^{th}$ order polynomial term, year, maximum daily temperature, change in maximum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, and change in binary precipitation (Table 1-7 and Table 1-*8*). Only maximum daily temperature had a large effect size (Figure 1-5, Table 1-8). Neither date nor year had a substantial effect on activity level (Table 1-8). Although also contained in the best supported model, change in maximum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, and change in binary precipitation had minimal effect sizes (Table 1-8). *Post-hoc* modelling indicated that an interaction between date and distance to hibernacula had a substantial effect on EPFU activity, such that activity levels decreased at distal sites more rapidly than proximal to hibernacula (Figure 6 and Table 1-9).

The best supported model describing MYSE activity contained the following variables: date, a 2$^{nd}$ order polynomial term on date, year, maximum daily temperature, change in maximum daily temperature, binary precipitation, change in binary precipitation, and distance to

cave (Table 1-10 and Table 1-*11*). Among those, date and distance to cave had the largest effect

sizes. Activity of MYSE was substantially greater proximal to cave entrances relative to distal

sites (Table 1-11). MYSE activity decreased over the season and maximum daily temperature

had a marginal positive impact on MYSE activity (Figure 1-7). MYSE activity was marginally

lower in 2016 than 2015 (Table 1-11). Although also contained in the best supported model,

change in maximum daily temperature, binary precipitation, and change in binary precipitation

had minimal effect sizes (Table 1-11). *Post-hoc* modelling indicated that an interaction between

date and distance to hibernacula had a substantial effect on MYSE activity, such that activity

levels decreased at distal sites more rapidly than proximal to hibernacula (Table 1-12, Figure 1-

8).

*The best supported model describing MYSO activity contained the following variables:*
*date, year, maximum daily temperature, change in maximum daily temperature, maximum daily*
*wind speed, change in maximum daily wind speed, binary precipitation, change in binary*
*precipitation, distance to cave, and an interaction between date and maximum daily temperature (*Table 1-13*). Among those,*
*date, year, distance to cave, mean maximum daily temperature, and the interaction between date and maximum daily*
*temperature had the largest effect sizes (*Table 1-13*). Activity of MYSO was substantially greater proximal to cave entrances*
*relative to distal sites and decreased over the season, but both were related positively to maximum daily temperature.*
*Temperature and date interacted, such that temperature had a stronger impact late in the season (*Figure 1-9*). Although*
*contained in the best supported model, change in maximum daily temperature, maximum daily wind speed, change in maximum*
*daily wind speed, binary precipitation, and change in binary precipitation had minimal effect sizes (*Table 1-13Table 1-
10: Rankings of models predicting *Myotis septentrionalis* (northern long-eared bat) activity
around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015
and 2016, with k (number of parameters), Akaike's information criteria (AIC) value, Akaike's
information criteria ($AIC_c$) value corrected for small sample size, difference in $AIC_c$ value
between best supported model and ith model ($\Delta AIC_c$), $w_i$ (model weight), and $ER_i$ (evidence
ratio).

| Variable | k | AIC | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $ER_i$ |
|---|---|---|---|---|---|---|
| Date + Date$^2$ + year + Max. Temp + $\Delta$ Max. Temp + Binary Precipitation + $\Delta$ Binary Precipitation + Cave Proximity | 9 | 2939 | 2939.2 | 0 | 0.369 | 1 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Date + Date$^2$ + year + Max. Temp + Max. Temp*Date + Δ Max. Temp + Binary Precipitation + Δ Binary Precipitation + Cave Proximity | 10 | 2939.1 | 2939.2 | 0.086 | 0.353 | 1.044 |

Table 1-11: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Myotis septentrionalis* (northern long-eared bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.

| Variable | β | Lower CI | Upper CI |
| --- | --- | --- | --- |
| (Intercept) | 1.355 | -0.446 | 3.156 |
| Date | -0.875 | -1.083 | -0.668 |
| Date$^2$ | -0.374 | -0.535 | -0.213 |
| year2016 | -0.340 | -0.674 | -0.006 |
| Max. Temp | 0.363 | 0.126 | 0.600 |
| Δ Max. Temp | -0.118 | -0.270 | 0.034 |
| Binary Precipitation1 | -0.195 | -0.519 | 0.129 |
| Δ Binary Precipitation | 0.046 | -0.275 | 0.366 |
| Distal Sites | -3.243 | -5.177 | -1.309 |

Table 1-12: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Myotis septentrionalis* (northern long-eared bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 1.535 | -0.254 | 3.325 |
| Date | -0.287 | -0.561 | -0.013 |
| Date$^2$ | -0.625 | -0.793 | -0.457 |
| Year 2016 | -0.385 | -0.702 | -0.067 |
| Max. Temp | 0.362 | 0.128 | 0.597 |
| Δ Max. Temp | -0.092 | -0.241 | 0.058 |
| Binary Precipitation1 | -0.194 | -0.503 | 0.114 |
| Δ Binary Precipitation | 0.089 | -0.217 | 0.395 |
| Distance to Cave1km | -2.647 | -4.848 | -0.446 |
| Distance to Cave2km | -5.016 | -7.305 | -2.728 |
| Distance to Cave3km | -3.554 | -5.692 | -1.417 |
| Date*Distance to Cave1km | -0.181 | -0.567 | 0.205 |
| Date*Distance to Cave2km | -2.258 | -2.832 | -1.684 |
| Date*Distance to Cave3km | -1.116 | -1.570 | -0.662 |

Table 1-*13*). Activity of MYSE was lower in 2016 than 2015. *Post-hoc* modelling indicated that an interaction between date and distance to hibernacula had a substantial effect on MYSO activity, such that activity levels early in autumn were higher at sites two and three km away from caves compared to sites one km away (Table 1-14). MYSO activity decreased more rapidly at these more distal sites than sites one km away from the cave (Table 1-14, Figure 1-10).

*Spring Activity Patterns*

The best supported model describing *Myotis* spp. activity contained the following variables: date and its 3rd order polynomial term, year, mean daily temperature, change in mean daily temperature, mean daily wind speed, change in mean daily wind speed, change in binary precipitation, distance to cave, and an interaction between date and mean daily temperature (Table 1-15). Among those, mean daily temperature, mean daily wind speed, and distance to cave had the largest effect sizes (Table 1-15). *Myotis* spp. activity was substantially greater proximal to cave entrances relative to distal sites (Table 1-15). *Myotis* spp. activity was consistently low over the season, only increasing slightly later in the spring, but neither date nor year had a substantial effect on activity level. *Myotis* spp. activity was related positively to mean daily temperature, but negatively related to mean daily wind speed. Temperature and date interacted, such that temperature had a stronger impact early in the season (Figure 1-11). Although also contained in the best supported model, change in mean daily temperature, change in mean daily wind speed, and change in binary precipitation had minimal effect sizes (Table 1-15). *Post-hoc* modelling indicated that there was no substantial interaction between date and distance to hibernacula (Table 1-16).

The best supported model describing 'cavebat' activity contained the following variables: date and its 3rd order polynomial, year, maximum daily temperature, minimum daily temperature,

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change in maximum daily temperature, change in minimum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, change in binary precipitation, distance to cave, and an interaction between date and maximum daily temperature (Table 1-17). Among those, maximum daily temperature and distance to cave had the largest effect sizes (Table 1-17). 'Cavebat' activity was positively related to maximum daily temperature, and substantially higher proximal to cave entrances relative to distal sites (Figure 1-12). Neither date nor year had a substantial effect on 'cavebat' activity level (Table 1-17). Although also contained in the best supported model, change in minimum daily temperature, change in minimum daily temperature, change in maximum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, change in binary precipitation, and the interaction between date and maximum daily temperature had minimal effect sizes (Table 1-17). *Post-hoc* modelling indicated that an interaction between date and distance to hibernacula had a substantial effect on 'cavebat' activity at sites two km away from caves, such that activity was lowest at sites two km away from caves early in the season but increased to be higher than sites one km away later in the season (Table 1-18, Figure 1-13).

The best supported model describing EPFU activity contained the following variables: date and its $3^{rd}$ order polynomial, year, maximum daily temperature, minimum daily temperature, change in maximum daily temperature, change in minimum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, change in binary precipitation, distance to cave, and an interaction between date and maximum daily temperature (Table 1-19). Among those, maximum daily temperature, binary precipitation, and distance to cave had the largest effect sizes (Table 1-19). Big brown bat activity was positively related to maximum daily temperature and negatively related to daily precipitation (Figure 1-14). Activity

was higher proximal to cave entrances relative to distal sites (Table 1-19). Neither date nor year had a substantial effect on EPFU activity level. Although also contained in the best supported model, minimum daily temperature, change in maximum daily temperature, change in minimum daily temperature, maximum daily wind speed, change in maximum daily wind speed, change in binary precipitation, and the interaction between date and maximum daily temperature had minimal effect sizes (Table 1-19). *Post-hoc* modelling indicated that an interaction between date and distance to hibernacula had a substantial effect on EPFU activity, such that activity levels increased at sites one km and two km away from hibernacula throughout the spring while activity proximal to hibernacula displayed a unimodal peak early in the season (Table 1-20, Figure 1-15).

The best supported model describing MYSE activity contained the following variables: date, year, maximum daily temperature, minimum daily temperature, change in maximum daily temperature, change in minimum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, change in binary precipitation, and distance to cave (Table 1-21). Among those, minimum daily temperature and distance to cave had the largest effect sizes (Table 1-21). MYSE activity was related positively to minimum daily temperature whereas activity was substantially greater proximal to cave entrances relative to distal sites (Figure 1-16). Neither date nor year had a substantial effect on MYSE activity level (Table 1-21). Although also contained in the best supported model, maximum daily temperature, change in maximum daily temperature, change in minimum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, and change in binary precipitation had minimal effect sizes (Table 1-21). *Post-hoc* modelling indicated that an interaction between date and distance to hibernacula had a substantial effect on MYSE activity,

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such that activity levels increased at most distal sites (two km and three km away) more rapidly than sites closer (one km away) and sites proximal to hibernacula (Table 1-22, Figure 1-17).

The best supported model describing MYSO activity contained the following variables: date and its 3<sup>rd</sup> order polynomial term, year, mean daily temperature, change in mean daily temperature, mean daily wind speed, change in mean daily wind speed, change in binary precipitation, distance to cave, and an interaction between date and mean daily temperature (Table 1-23). Among those, mean daily temperature, mean daily wind speed, distance to cave, and the interaction between date and mean daily temperature had the largest effect sizes (Table 1-23). Mean daily temperature and date interacted such that temperature had a greater impact earlier in the season (Figure 1-18). Indiana bat activity was positively related to mean daily temperature, but negatively related to mean daily wind speed (Figure 1-19). Indiana bat activity was substantially greater proximal to cave entrances relative to distal sites (Table 1-23). Neither date alone nor year had a substantial effect on MYSO activity level. Although also contained in the best supported model, change in mean daily temperature, change in mean wind speed, and change in binary precipitation had minimal effect sizes (Table 1-23). *Post-hoc* modelling indicated that there was no substantial interaction between date and distance to hibernacula (Table 1-24).

*Discussion*

Autumn activity varied among species and among species groups, but my results largely were consistent with *a priori* expectations. In general, bat activity was most related to ambient temperatures during autumn. In spring, bat activity was most related to ambient temperatures, but related less closely to date. Based on differing life histories, I expected species-specific responses to ambient conditions and distance to caves in temperate environments (Aldridge and

Rautenbach 1987, Bergeson et al. 2013, Jachowski et al. 2014, Norquay and Willis 2014). The results corroborate previous research indicating ambient temperatures are positively related to general bat activity across seasons (Parsons et al. 2003, Kunz 2013, Bender and Hartman 2015, Meyer et al. 2016, Bernard and McCracken 2017), and specifically show this relationship exists around hibernacula.

Although temperature and date generally had large effects on overall bat activity, not all species/groups followed this exact pattern. I expected *a priori* that activity for all individual cave-dwelling species would contract and concentrate around cave entrances through autumn, but my results indicated this pattern existed only for MYSO, MYSE and EPFU. The substantial interacting effects of temperature and date on *Myotis* spp., 'cavebats', and MYSO autumn activity likely exist due to metabolic/thermal costs and/or benefits relating to prey availability (Bender and Hartman 2015, Bernard and McCracken 2017). Prey resources of insectivorous bats become scarce at lower ambient temperatures (Williams 1940, Meyer et al. 2016). Autumn activity of EPFU largely depended on maximum daily temperature, a finding similar to previous research indicating EPFU activity through the winter months is influenced by temperature (Klüg-Baerwald et al. 2016). Research has found that unlike *Myotis* spp., EPFU appear to be less impacted by WNS (Francl et al. 2012), and may have fewer physiological constraints due to larger body sizes, allowing for greater proportional late fall and winter energy expenditures during the hibernation season therefore there was no evidence of interacting effects of temperature and date on EPFU. It is possible EPFU can also return to typical summer-type roosts (human structures/barns) during fall and winter activity, which may afford thermal and metabolic benefits (Whitaker Jr. and Gummer 1992). The best supported model did not include the at-cave variable, indicating that EPFU activity was generally more widespread across the landscape

during autumn. This is in contrast with other cave-dwelling species and species group in my study. This is likely a result of species-specific foraging strategies, but also could be attributed to species-specific roost selection and preference; EPFU may fly over 1.6 km to foraging areas from roost sites, further, on average, than the *Myotis* spp. that occurred at my study sites (Brigham 1991, Menzel et al. 2002, 2005, Lowe 2012). The verified (Brack et al. 2005, Powers et al. 2015) and speculative (Weishampel et al. 2011) existence of other hibernacula in close proximity (within 3 km) to my study sites might have had an influence on each of the species and species groups through the autumn swarm period.

The majority of activity for all species/groups occurred in early autumn and declined by mid-October, yet some activity (across species/groups) continued to occur through the fall swarm season at warmer conditions, suggesting that ambient conditions may partially regulate swarm activity and cave entry dynamics. Furthermore, by influencing bat activity and prey availability, ambient temperature may ultimately influence the body condition of bats entering hibernation (Hall 1962, Jonasson and Willis 2011). In any given year, above-average ambient temperatures may delay bats' entry into hibernation by allowing bats to remain active later in autumn. This could presumably lead to shorter hibernation periods; potentially reducing fungal loads and therefore WNS-related mortality (Reeder et al. 2012, Langwig et al. 2015). Warmer temperatures are linked to increased prey availability (Meyer et al. 2016*a*) and may lead to superior body conditions as bats enter hibernation, which also may affect overwinter survival as well as reproductive output in the following seasons (Frick et al. 2012). Conversely, it may be that colder ambient temperatures during the pre-hibernation period lead to improved fat reserves, as seen in a European bat species, the brown long-eared bat (*Plecotus auritus*; Speakman and Rowland 1999). Prior to hibernation, warmer temperatures lead to greater activity on the

landscape, but this could cause bats to be susceptible to other threats such as wind energy development or forest management, if day-roost loss occurred later into autumn than previously anticipated. Furthermore, the exact biological triggers for immergence into hibernation are not fully understood for bats, and these triggers may be more closely linked to fat reserves than to ambient conditions and/or prey availability (Jonasson and Willis 2011). Although cave-dwelling bats, and specifically MYSO, usually hibernate where they swarm (LaVal et al. 1977, Schaik et al. 2015), pre-hibernation long-distance movements between hibernacula/swarming sites are not uncommon (Cope and Humphrey 1977, Parsons et al. 2003). Ambient temperatures could certainly affect the movement patterns of bats between hibernacula/swarming sites, and thus may affect mating dynamics and immergence phenology. Further understanding the effects of temperature on swarming behavior may allow managers to determine the most crucial swarming periods, and thus plan protective measures around hibernacula more efficiently.

Similar to autumn, spring activity also was species-specific, but in general, activity was less related to date. Daily temperatures were the driving climatic variable that impacted activity for all species and groups in the spring, supporting *a priori* expectations. Findings also agreed with previous research that showed bat emergence from hibernacula in the spring was related positively to ambient temperatures and, to a lesser extent, photoperiod (Meyer et al. 2016). Czenze and Willis (2015) found MYLU spring emergence was correlated most with a drop in barometric pressure, rather than temperatures outside a hibernacula. Furthermore, Meyer et al. (2016) found that timing of emergence was not associated with temperatures inside hibernacula. However, I found that ambient temperatures substantially affect bat activity post-emergence, across species/groups. Temperatures at roost sites within hibernacula change very little regardless of changing outside ambient temperatures (Czenze and Willis 2015, Meyer et al.

2016), but temperatures and temperature fluctuations at roost sites outside hibernacula are readily perceived by bats (Hamilton and Barclay 1994, Callahan et al. 1997). Ambient temperatures post-emergence likely are the principal indicators for bats' activity in the spring.

Although the effect size of date in spring was smaller than in autumn, there was an interaction between date and distance to hibernacula for 'cavebats', MYSE, and EPFU. Activity of 'cavebats' at distal sites increased at different rates towards the end of April, possibly reflecting the progression of movement of bats outwards from hibernacula towards summer ranges. Similarly, by mid-April, MYSE activity increased at a greater rate at most distal sites (2 and 3 km away) whereas activity decreased at sites one km from caves, likely displaying an outward movement of bats post-emergence. Spring activity of EPFU followed a comparable trend, with activity increasing faster at distal sites than at sites proximal to caves. Although the interaction between date and distance to hibernacula had large effect sizes, confidence intervals for estimates of 'cavebats', MYSE, and EPFU activity were large and overlapping, suggesting small trends.

Northern long-eared bat activity was most related to minimum daily temperature whereas activity of all other species/groups activity was more closely related to mean daily or maximum daily temperature likely due to species-specific foraging strategies and differences in prey base (Aldridge and Rautenbach 1987, Lacki et al. 2007). Lepidopterans (moths and butterflies) are important prey of MYSE (Caceres and Barclay 2000, Carter et al. 2003, Dodd et al. 2012) and are less active at cooler temperatures and generally less abundant during the dormant, non-growing season (Williams 1940, Meyer et al. 2016). However, data on MYSE prey selection are limited and chiefly from summer months, with knowledge of prey resources in the spring lacking (Carter et al. 2003, Dodd et al. 2012). It is possible that MYSE may perceive minimum daily

temperatures as an indicator of prey availability whereas other species more readily perceive maximum or mean daily temperatures as indicators of prey availability (Wojciechowski et al. 2007). Further research is warranted on spring prey availability in relation to temperature to determine how and why temperature drives species-specific activity patterns during the spring emergence period (Ciechanowski et al. 2007).

Although the USFWS seasonal tree clearing window allows clearing activities through March 31$^{st}$, I observed a substantial amount of activity of MYSO and all cave-dwelling species well before the end of March. Furthermore, many hibernacula are used by both MYSO and MYSE during the winter months, and summer ranges overlap significantly (Trani et al. 2007, USFWS 2015, 2017*b*). I observed extremely low MYSE activity relative to other species, including MYSO, which supports previous research indicating MYSE are among the species most impacted by WNS and are functionally absent in many parts of the region (Francl et al. 2012, Powers et al. 2015, Reynolds et al. 2016). These results suggest that tree-clearing activities in the spring could affect MYSO and MYSE in the central Appalachians, especially when early spring temperatures are unseasonably warm. Tree-clearing activities during the spring near hibernacula prior to March 31 may have the potential, albeit it small, to exacerbate WNS-related population declines in the central Appalachians. Alternately, my data support the adequacy of the spatial and temporal extent of these buffers during the autumn swarm season, as activity had declined to negligible levels prior to the November 15$^{th}$ clearing date. Currently, the Indiana Bat Protection and Enhancement Plan Guidelines (USFWS 2009) provides for flexibility and adjustments to tree clearing restriction dates based on localized fall swarming and spring emergence data within the range of MYSO. However, data regarding bat activity around hibernacula during these seasons are scant, offering few incentives to change the clearing

restriction dates. Due to the physiological vulnerability of bats following hibernation when their fat reserves are depleted most and prey resources are less abundant or highly variable in availability, managers should prioritize maintaining habitats surrounding hibernacula to ensure adequate foraging and roosting opportunities.

Current land use and/or active land management around hibernacula may impact both MYSE and MYSO during the autumn and spring. Prior to WNS, many of these impacts could have been considered negligible, but additive mortality factors could further imperil already diminutive populations following the impacts of WNS. My data suggest that concluding tree-clearing activities by early March could more adequately protect physiologically-stressed MYSO as they resume behaviors on the landscape. Streamlining management strategies will increase the chance for populations' persistence and recovery by avoiding 'take' in seasons critical for successful reproduction. Extending these protections to a number of hibernacula also would undoubtedly benefit other imperiled bat species' populations not considered here. Finally, a better regional comprehension of the effects of ambient conditions on autumn and spring bat activity will help land managers and researchers plan effective surveys to further understand post-WNS ecology of bats.

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Table 1-1: Variables used in candidate models representing hypotheses regarding bat activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016, and spring 2016 and 2017. Variables were used in different combinations, and highly correlated variables were not included within a single candidate model.

| Variable | Explanation |
| --- | --- |
| Date | date |
| Year | sampling year |
| Avg. Temp | mean daily temperature |
| Max. Temp | maximum daily temperature |
| Min. Temp | minimum daily temperature |
| Δ Avg. Temp | change in mean daily temperature from previous day |
| Δ Max. Temp | change in maximum daily temperature from previous day |
| Δ Min. Temp | change in minimum daily temperature from previous day |
| Max Wind | maximum daily wind speed |
| Avg. Wind | mean daily wind speed |
| Δ Max. Wind | change in maximum daily wind speed from previous day |
| Δ Mean. Wind | change in mean daily wind speed from previous day |
| Binary Precipitation | binary precipitation |
| Δ Binary Precipitation | change in binary precipitation from previous day |
| Cave Proximity | at cave or not at cave |

Table 1-2: Variables used in candidate models describing bat activity with justification and supporting literature for each parameter. Candidate models represented hypotheses regarding bat activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016, and spring 2016 and 2017.

| Parameter | Justification | Supporting Literature |
|---|---|---|
| Date | Bat activity varies in intensity and spatially by date | (Parsons et al. 2003, Brack 2006, Brooks 2009, Johnson et al. 2011) |
| Year | Bat abundance and activity varies from year to year, especially in the wake of WNS | (Blehert et al. 2009, Frick et al. 2010, Francl et al. 2012) |
| Mean daily temperature | Daily temperatures affect bat activity | (Parsons et al. 2003, Bender and Hartman 2015, Meyer et al. 2016) |
| Maximum daily temperature | Daily temperatures affect bat activity | (Parsons et al. 2003, Bender and Hartman 2015, Meyer et al. 2016) |
| Minimum daily temperature | Daily temperatures affect bat activity | (Parsons et al. 2003, Bender and Hartman 2015, Meyer et al. 2016) |
| Change in mean daily temperature from previous day | Bats can likely sense even small temperature changes and could adjust behavior accordingly | (Kunz 2013, Meyer et al. 2016) |
| Change in maximum daily temperature from previous day | Bats can likely sense even small temperature changes and could adjust behavior accordingly | (Kunz 2013, Meyer et al. 2016) |
| Change in minimum daily temperature from previous day | Bats can likely sense even small temperature changes and could adjust behavior accordingly | (Kunz 2013, Meyer et al. 2016) |
| Maximum daily wind speed | Bat activity generally decreases with high wind speeds | (Baerwald and Barclay 2011, Weller and Baldwin 2012, Smith and McWilliams 2016) |

*Table 1-2 (Continued)*

| Parameter | Justification | Supporting Literature |
|---|---|---|
| Mean daily wind speed | Bat activity generally decreases with high wind speeds | (Baerwald and Barclay 2011, Weller and Baldwin 2012, Smith and McWilliams 2016) |
| Change in maximum daily wind speed from previous day | Bats likely perceive changes in wind speed and adjust behavior accordingly | (Baerwald and Barclay 2011, Weller and Baldwin 2012, Smith and McWilliams 2016) |
| Change in mean daily wind speed from previous day | Bats likely perceive changes in wind speed and adjust behavior accordingly | (Baerwald and Barclay 2011, Weller and Baldwin 2012, Smith and McWilliams 2016) |
| Daily binary precipitation | Precipitation reduces bat activity | (Parsons et al. 2003, Kunz 2013) |
| Change in daily binary precipitation from previous day | Bats likely perceive a changes in precipitation and adjust behavior accordingly | (Parsons et al. 2003, Kunz 2013) |
| At cave/not at cave | Activity is concentrated at hibernacula entrances | (Burns and Broders 2015, Schaik et al. 2015) |

Table 1-3: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Myotis* species' (*Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.848 | 2.046 | 5.651 |
| Date | -0.810 | -0.958 | -0.661 |
| Date$^2$ | -0.057 | -0.186 | 0.072 |
| Year 2016 | -0.516 | -0.717 | -0.316 |
| Avg. Temp | 0.493 | 0.336 | 0.650 |
| Δ Avg. Temp | -0.204 | -0.300 | -0.107 |
| Avg. Wind | -0.143 | -0.305 | 0.020 |
| Δ Mean. Wind | -0.143 | -0.265 | -0.022 |
| Δ Binary Precipitation | -0.302 | -0.489 | -0.116 |
| Distal Sites | -3.095 | -4.609 | -1.582 |
| Date*Avg. Temp | 0.466 | 0.315 | 0.616 |

Table 1-4: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Myotis* species' (*Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.881 | 2.068 | 5.694 |
| Date | -0.661 | -0.927 | -0.394 |
| Date$^2$ | -0.061 | -0.190 | 0.068 |
| Year 2016 | -0.519 | -0.720 | -0.318 |
| Avg. Temp | 0.499 | 0.341 | 0.657 |
| Δ Avg. Temp | -0.205 | -0.302 | -0.107 |
| Avg. Wind | -0.144 | -0.306 | 0.019 |
| Δ Mean. Wind | -0.141 | -0.263 | -0.020 |
| Δ Binary Precipitation | -0.303 | -0.490 | -0.117 |
| Distal Sites | -3.129 | -4.647 | -1.610 |
| Date*Avg. Temp | 0.477 | 0.325 | 0.630 |
| Date*Cave Proximity | -0.181 | -0.451 | 0.088 |

Table 1-5: Estimates and 95% confidence intervals (CI) from the best supported model predicting 'cavebat' species' (*Eptesicus fuscus,* big brown bat; *Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat; *Perimyotis subflavus,* eastern tricolored bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.855 | 2.271 | 5.439 |
| Date | -0.664 | -0.793 | -0.535 |
| Date$^2$ | 0.036 | -0.077 | 0.150 |
| Year 2016 | -0.432 | -0.613 | -0.250 |
| Avg. Temp | 0.638 | 0.499 | 0.776 |
| Δ Avg. Temp | -0.145 | -0.231 | -0.059 |
| Avg. Wind | -0.028 | -0.166 | 0.111 |
| Δ Mean. Wind | -0.131 | -0.238 | -0.024 |
| Δ Binary Precipitation | -0.418 | -0.587 | -0.250 |
| Distal Sites | -2.667 | -3.955 | -1.378 |
| Date*Avg. Temp | 0.413 | 0.284 | 0.543 |

Table 1-6: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting 'cavebat' species' (*Eptesicus fuscus,* big brown bat; *Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat; *Perimyotis subflavus,* eastern tricolored bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.824 | 2.24 | 5.408 |
| Date | -0.493 | -0.742 | -0.244 |
| Date$^2$ | 0.109 | -0.125 | 0.344 |
| Year 2016 | -0.433 | -0.614 | -0.252 |
| Avg. Temp | 0.643 | 0.504 | 0.782 |
| Δ Avg. Temp | -0.152 | -0.238 | -0.067 |
| Avg. Wind | -0.043 | -0.181 | 0.096 |
| Δ Mean. Wind | -0.129 | -0.235 | -0.022 |
| Δ Binary Precipitation | -0.412 | -0.581 | -0.243 |
| Distance to Cave1km | -2.492 | -3.976 | -1.009 |
| Distance to Cave2km | -2.951 | -4.435 | -1.467 |
| Distance to Cave3km | -2.532 | -3.963 | -1.102 |
| Date*Avg. Temp | 0.432 | 0.3 | 0.565 |
| Date*Distance to Cave1km | -0.119 | -0.416 | 0.179 |
| Date*Distance to Cave2km | -0.113 | -0.389 | 0.162 |
| Date*Distance to Cave3km | -0.378 | -0.663 | -0.093 |
| Date$^2$*Distance to Cave1km | -0.188 | -0.458 | 0.081 |
| Date$^2$*Distance to Cave2km | 0.119 | -0.143 | 0.381 |
| Date$^2$*Distance to Cave3km | -0.182 | -0.443 | 0.079 |

Table 1-7: Rankings of models predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016, with k (number of parameters), Akaike's information criteria (AIC) value, Akaike's information criteria (AIC$_c$) value corrected for small sample size, difference in AIC$_c$ value between best supported model and ith model ($\Delta$AIC$_c$), w$_i$ (model weight), and ER$_i$ (evidence ratio).

| Variable | k | AIC | AIC$_c$ | $\Delta$AIC$_c$ | $w_i$ | $ER_i$ |
|---|---|---|---|---|---|---|
| Date + Date$^2$ + Date$^3$ + Date$^4$ + year + Max. Temp + $\Delta$ Max. Temp + Max Wind + $\Delta$ Max. Wind + Binary Precipitation + $\Delta$ Binary Precipitation | 12.0 | 3699.4 | 3699.6 | 0.0 | 0.5 | 1.0 |
| Date + Date$^2$ + Date$^3$ + Date$^4$ + year +Date*Max. Temp + Min. Temp + $\Delta$ Max. Temp + $\Delta$ Min. Temp + Max Wind + $\Delta$ Max. Wind + Binary Precipitation + $\Delta$ Binary Precipitation + Cave Proximity | 16.0 | 3700.5 | 3700.9 | 1.3 | 0.2 | 1.9 |
| Date + Date$^2$ + Date$^3$ + Date$^4$ + year + Max. Temp + $\Delta$ Max. Temp + Max Wind + $\Delta$ Max. Wind + Binary Precipitation + $\Delta$ Binary Precipitation + Cave Proximity | 13.0 | 3701.0 | 3701.2 | 1.6 | 0.2 | 2.3 |

Table 1-8: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.

| Variable | β | Lower CI | Upper CI |
| --- | --- | --- | --- |
| (Intercept) | -1.298 | -2.049 | -0.547 |
| Date | 0.071 | -0.222 | 0.364 |
| Date$^2$ | 0.139 | -0.257 | 0.534 |
| Date$^3$ | -0.114 | -0.243 | 0.016 |
| Date$^4$ | -0.056 | -0.182 | 0.070 |
| Year 2016 | -0.038 | -0.340 | 0.264 |
| Max. Temp | 1.222 | 0.983 | 1.462 |
| Δ Max. Temp | 0.165 | 0.012 | 0.318 |
| Max Wind | 0.296 | 0.109 | 0.483 |
| Δ Max. Wind | -0.068 | -0.240 | 0.104 |
| Binary Precipitation1 | -0.201 | -0.509 | 0.108 |
| Δ Binary Precipitation | -0.230 | -0.549 | 0.089 |

Table 1-9: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
| --- | --- | --- | --- |
| (Intercept) | -0.704 | -2.541 | 1.132 |
| Date | 0.941 | 0.509 | 1.373 |
| Date$^2$ | 0.006 | -0.378 | 0.390 |
| Date$^3$ | -0.131 | -0.262 | 0.000 |
| Date$^4$ | -0.028 | -0.151 | 0.094 |
| Year 2016 | 0.010 | -0.283 | 0.303 |
| Max. Temp | 1.213 | 0.977 | 1.449 |
| Δ Max. Temp | 0.140 | -0.009 | 0.290 |
| Max Wind | 0.202 | 0.018 | 0.386 |
| Δ Max. Wind | -0.094 | -0.263 | 0.075 |
| Binary Precipitation1 | -0.197 | -0.500 | 0.106 |
| Δ Binary Precipitation | -0.247 | -0.561 | 0.067 |
| Distance to Cave1km | -1.380 | -3.609 | 0.849 |
| Distance to Cave2km | -0.611 | -2.825 | 1.604 |
| Distance to Cave3km | -0.245 | -2.384 | 1.894 |
| Date*Distance to Cave1km | -0.821 | -1.245 | -0.397 |
| Date*Distance to Cave2km | -0.728 | -1.108 | -0.348 |
| Date*Distance to Cave3km | -1.230 | -1.610 | -0.850 |

Table 1-10: Rankings of models predicting *Myotis septentrionalis* (northern long-eared bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016, with k (number of parameters), Akaike's information criteria (AIC) value, Akaike's information criteria ($AIC_c$) value corrected for small sample size, difference in $AIC_c$ value between best supported model and ith model ($\Delta AIC_c$), $w_i$ (model weight), and $ER_i$ (evidence ratio).

| Variable | k | AIC | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $ER_i$ |
|---|---|---|---|---|---|---|
| Date + Date$^2$ + year + Max. Temp + $\Delta$ Max. Temp + Binary Precipitation + $\Delta$ Binary Precipitation + Cave Proximity | 9 | 2939 | 2939.2 | 0 | 0.369 | 1 |
| Date + Date$^2$ + year + Max. Temp + Max. Temp*Date + $\Delta$ Max. Temp + Binary Precipitation + $\Delta$ Binary Precipitation + Cave Proximity | 10 | 2939.1 | 2939.2 | 0.086 | 0.353 | 1.044 |

Table 1-11: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Myotis septentrionalis* (northern long-eared bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.

| Variable | β | Lower CI | Upper CI |
| --- | --- | --- | --- |
| (Intercept) | 1.355 | -0.446 | 3.156 |
| Date | -0.875 | -1.083 | -0.668 |
| Date$^2$ | -0.374 | -0.535 | -0.213 |
| year2016 | -0.340 | -0.674 | -0.006 |
| Max. Temp | 0.363 | 0.126 | 0.600 |
| Δ Max. Temp | -0.118 | -0.270 | 0.034 |
| Binary Precipitation1 | -0.195 | -0.519 | 0.129 |
| Δ Binary Precipitation | 0.046 | -0.275 | 0.366 |
| Distal Sites | -3.243 | -5.177 | -1.309 |

Table 1-12: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Myotis septentrionalis* (northern long-eared bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 1.535 | -0.254 | 3.325 |
| Date | -0.287 | -0.561 | -0.013 |
| Date$^2$ | -0.625 | -0.793 | -0.457 |
| Year 2016 | -0.385 | -0.702 | -0.067 |
| Max. Temp | 0.362 | 0.128 | 0.597 |
| Δ Max. Temp | -0.092 | -0.241 | 0.058 |
| Binary Precipitation1 | -0.194 | -0.503 | 0.114 |
| Δ Binary Precipitation | 0.089 | -0.217 | 0.395 |
| Distance to Cave1km | -2.647 | -4.848 | -0.446 |
| Distance to Cave2km | -5.016 | -7.305 | -2.728 |
| Distance to Cave3km | -3.554 | -5.692 | -1.417 |
| Date*Distance to Cave1km | -0.181 | -0.567 | 0.205 |
| Date*Distance to Cave2km | -2.258 | -2.832 | -1.684 |
| Date*Distance to Cave3km | -1.116 | -1.570 | -0.662 |

Table 1-13: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Myotis sodalis* (Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 2.588 | 0.694 | 4.481 |
| Date | -0.726 | -0.909 | -0.543 |
| Year 2016 | -0.869 | -1.117 | -0.621 |
| Max. Temp | 0.846 | 0.647 | 1.046 |
| Δ Max. Temp | -0.128 | -0.252 | -0.003 |
| Max Wind | -0.139 | -0.307 | 0.029 |
| Δ Max. Wind | -0.263 | -0.415 | -0.112 |
| Binary Precipitation1 | -0.056 | -0.315 | 0.204 |
| Δ Binary Precipitation | 0.056 | -0.210 | 0.322 |
| Distal Sites | -3.142 | -4.745 | -1.539 |
| Date*Max. Temp | 0.544 | 0.382 | 0.705 |

Table 1-14: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Myotis sodalis* (Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 2.631 | 0.720 | 4.542 |
| Date | -0.475 | -0.776 | -0.174 |
| Year 2016 | -0.863 | -1.108 | -0.618 |
| Max. Temp | 0.851 | 0.651 | 1.050 |
| Δ Max. Temp | -0.129 | -0.253 | -0.005 |
| Max Wind | -0.168 | -0.335 | 0.000 |
| Δ Max. Wind | -0.276 | -0.427 | -0.126 |
| Binary Precipitation1 | -0.030 | -0.288 | 0.227 |
| Δ Binary Precipitation | 0.041 | -0.224 | 0.305 |
| Distance to Cave1km | -2.628 | -4.421 | -0.835 |
| Distance to Cave2km | -3.658 | -5.486 | -1.830 |
| Distance to Cave3km | -3.433 | -5.185 | -1.681 |
| Date*Max. Temp | 0.605 | 0.437 | 0.773 |
| Date*Distance to Cave1km | 0.009 | -0.369 | 0.387 |
| Date*Distance to Cave2km | -0.579 | -0.955 | -0.203 |
| Date*Distance to Cave3km | -0.412 | -0.810 | -0.014 |

Table 1-15: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Myotis* species' (*Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.624 | 1.746 | 5.501 |
| Date | -0.216 | -0.442 | 0.010 |
| Date$^2$ | -0.003 | -0.104 | 0.099 |
| Date$^3$ | 0.243 | 0.141 | 0.345 |
| Year 2017 | -0.010 | -0.239 | 0.219 |
| Avg. Temp | 0.904 | 0.761 | 1.047 |
| Δ Avg. Temp | -0.266 | -0.373 | -0.158 |
| Avg. Wind | -0.507 | -0.670 | -0.343 |
| Δ Mean. Wind | 0.068 | -0.064 | 0.201 |
| Δ Binary Precipitation | -0.125 | -0.331 | 0.080 |
| Distal Sites | -3.384 | -5.391 | -1.377 |
| Date*Avg. Temp | -0.471 | -0.591 | -0.351 |

Table 1-16: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Myotis* species' (*Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.629 | 1.708 | 5.549 |
| Date | -0.195 | -0.635 | 0.245 |
| Date$^2$ | -0.194 | -0.384 | -0.005 |
| Date$^3$ | 0.110 | -0.067 | 0.287 |
| Year 2017 | -0.070 | -0.307 | 0.168 |
| Avg. Temp | 0.891 | 0.743 | 1.039 |
| Δ Avg. Temp | -0.275 | -0.387 | -0.163 |
| Avg. Wind | -0.458 | -0.629 | -0.288 |
| Δ Mean. Wind | 0.075 | -0.061 | 0.212 |
| Δ Binary Precipitation | -0.059 | -0.269 | 0.152 |
| Distance to Cave1km | -3.462 | -5.804 | -1.120 |
| Distance to Cave2km | -4.251 | -6.620 | -1.881 |
| Distance to Cave3km | -2.754 | -5.001 | -0.507 |
| Date*Distance to Cave1km | 0.129 | -0.486 | 0.743 |
| Date*Distance to Cave2km | -0.082 | -0.735 | 0.570 |
| Date*Distance to Cave3km | 0.153 | -0.460 | 0.765 |
| Date$^2$*Distance to Cave1km | 0.293 | 0.034 | 0.552 |
| Date$^2$*Distance to Cave2km | 0.187 | -0.080 | 0.454 |
| Date$^2$*Distance to Cave3km | 0.003 | -0.259 | 0.264 |
| Date$^3$*Distance to Cave1km | -0.030 | -0.287 | 0.227 |
| Date$^3$*Distance to Cave2km | 0.170 | -0.099 | 0.440 |
| Date$^3$*Distance to Cave3km | -0.120 | -0.381 | 0.140 |

Table 1-17: Estimates and 95% confidence intervals (CI) from the best supported model predicting 'cavebat' species' (*Eptesicus fuscus,* big brown bat; *Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat; *Perimyotis subflavus,* eastern tricolored bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.769 | 1.865 | 5.674 |
| Date | -0.120 | -0.318 | 0.078 |
| Date$^2$ | -0.045 | -0.129 | 0.040 |
| Date$^3$ | 0.151 | 0.066 | 0.236 |
| Year 2017 | -0.282 | -0.486 | -0.079 |
| Max. Temp | 1.011 | 0.817 | 1.205 |
| Min. Temp | 0.396 | 0.210 | 0.581 |
| Δ Max. Temp | -0.139 | -0.275 | -0.003 |
| Δ Min. Temp | 0.004 | -0.099 | 0.107 |
| Max Wind | -0.448 | -0.565 | -0.332 |
| Δ Max. Wind | -0.072 | -0.183 | 0.040 |
| Binary Precipitation1 | -0.120 | -0.323 | 0.083 |
| Δ Binary Precipitation | 0.066 | -0.138 | 0.271 |
| Distal Sites | -2.823 | -4.848 | -0.799 |
| Date*Max. Temp | -0.195 | -0.294 | -0.095 |

Table 1-18: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting 'cavebat' species' (*Eptesicus fuscus,* big brown bat; *Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat; *Perimyotis subflavus,* eastern tricolored bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 3.922 | 2.072 | 5.773 |
| Date | -0.447 | -0.849 | -0.044 |
| Date$^2$ | -0.223 | -0.389 | -0.056 |
| Date$^3$ | 0.196 | 0.034 | 0.359 |
| Year 2017 | -0.242 | -0.445 | -0.038 |
| Max. Temp | 1.001 | 0.804 | 1.198 |
| Min. Temp | 0.406 | 0.218 | 0.594 |
| Δ Min. Temp | 0.006 | -0.097 | 0.109 |
| Δ Max. Temp | -0.135 | -0.270 | 0.001 |
| Max Wind | -0.443 | -0.560 | -0.326 |
| Δ Max. Wind | -0.070 | -0.180 | 0.040 |
| Binary Precipitation1 | -0.136 | -0.337 | 0.066 |
| Δ Binary Precipitation | 0.036 | -0.166 | 0.239 |
| Distance to Cave1km | -3.204 | -5.450 | -0.957 |
| Distance to Cave2km | -3.747 | -6.003 | -1.491 |
| Distance to Cave3km | -2.362 | -4.513 | -0.210 |
| Date*Distance to Cave1km | 0.412 | -0.130 | 0.954 |
| Date*Distance to Cave2km | 0.668 | 0.103 | 1.234 |
| Date*Distance to Cave3km | 0.325 | -0.203 | 0.853 |
| Date$^2$*Distance to Cave1km | 0.278 | 0.052 | 0.503 |
| Date$^2$*Distance to Cave2km | 0.296 | 0.072 | 0.521 |
| Date$^2$*Distance to Cave3km | 0.044 | -0.169 | 0.257 |
| Date$^3$*Distance to Cave1km | -0.108 | -0.334 | 0.118 |
| Date$^3$*Distance to Cave2km | -0.070 | -0.302 | 0.161 |
| Date$^3$*Distance to Cave3km | -0.091 | -0.307 | 0.124 |
| Date*Max. Temp | -0.212 | -0.315 | -0.108 |

Table 1-19: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 0.040 | -2.346 | 2.427 |
| Date | -0.087 | -0.404 | 0.231 |
| Date$^2$ | -0.213 | -0.336 | -0.089 |
| Date$^3$ | 0.160 | 0.033 | 0.287 |
| Year 2017 | -0.440 | -0.767 | -0.114 |
| Max. Temp | 1.501 | 1.155 | 1.847 |
| Min. Temp | 0.381 | 0.104 | 0.657 |
| Δ Max. Temp | 0.008 | -0.201 | 0.217 |
| Δ Min. Temp | -0.072 | -0.223 | 0.080 |
| Max Wind | -0.122 | -0.305 | 0.062 |
| Δ Max. Wind | 0.119 | -0.068 | 0.305 |
| Binary Precipitation1 | -0.516 | -0.819 | -0.214 |
| Δ Binary Precipitation | -0.079 | -0.383 | 0.225 |
| Distal Sites | -0.654 | -3.184 | 1.876 |
| Date*Max. Temp | -0.077 | -0.269 | 0.115 |

Table 1-20: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 0.048 | -2.212 | 2.308 |
| Date | -0.633 | -1.016 | -0.249 |
| Date$^2$ | -0.220 | -0.343 | -0.098 |
| Date$^3$ | 0.185 | 0.060 | 0.311 |
| Year 2017 | -0.447 | -0.773 | -0.122 |
| Max. Temp | 1.535 | 1.191 | 1.878 |
| Min. Temp | 0.398 | 0.116 | 0.679 |
| Δ Min. Temp | -0.058 | -0.212 | 0.095 |
| Δ Max. Temp | 0.001 | -0.209 | 0.211 |
| Max Wind | -0.075 | -0.259 | 0.110 |
| Δ Max. Wind | 0.150 | -0.033 | 0.334 |
| Binary Precipitation1 | -0.536 | -0.837 | -0.236 |
| Δ Binary Precipitation | -0.104 | -0.406 | 0.198 |
| Distance to Cave1km | -1.418 | -4.138 | 1.302 |
| Distance to Cave2km | -1.152 | -3.874 | 1.570 |
| Distance to Cave3km | 0.143 | -2.459 | 2.746 |
| Date*Distance to Cave1km | 0.979 | 0.597 | 1.361 |
| Date*Distance to Cave2km | 0.718 | 0.358 | 1.079 |
| Date*Distance to Cave3km | 0.424 | 0.079 | 0.770 |
| Date*Max. Temp | -0.122 | -0.312 | 0.068 |

Table 1-21: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Myotis septentrionalis* (northern long-eared bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 1.012 | -0.563 | 2.587 |
| Date | 0.244 | 0.076 | 0.412 |
| Year 2017 | -0.206 | -0.561 | 0.150 |
| Max. Temp | 0.411 | 0.052 | 0.769 |
| Min. Temp | 0.541 | 0.228 | 0.853 |
| Δ Max. Temp | -0.261 | -0.492 | -0.030 |
| Δ Min. Temp | 0.047 | -0.129 | 0.223 |
| Max Wind | -0.274 | -0.467 | -0.081 |
| Δ Max. Wind | 0.068 | -0.130 | 0.265 |
| Binary Precipitation1 | -0.252 | -0.620 | 0.117 |
| Δ Binary Precipitation | -0.122 | -0.486 | 0.241 |
| Distal Sites | -3.091 | -4.741 | -1.441 |

Table 1-22: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Myotis septentrionalis* (northern long-eared bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 0.904 | -0.672 | 2.480 |
| Date | 0.065 | -0.156 | 0.286 |
| Date$^2$ | -0.052 | -0.196 | 0.092 |
| Year 2017 | -0.164 | -0.510 | 0.181 |
| Max. Temp | 0.889 | 0.660 | 1.118 |
| Δ Max. Temp | -0.007 | -0.183 | 0.170 |
| Binary Precipitation1 | -0.173 | -0.490 | 0.145 |
| Δ Binary Precipitation | 0.053 | -0.271 | 0.376 |
| Distance to Cave1km | -3.105 | -4.987 | -1.223 |
| Distance to Cave2km | -4.004 | -5.952 | -2.057 |
| Distance to Cave3km | -2.746 | -4.537 | -0.955 |
| Date*Distance to Cave1km | -0.288 | -0.668 | 0.092 |
| Date*Distance to Cave2km | 0.976 | 0.505 | 1.448 |
| Date*Distance to Cave3km | 0.694 | 0.293 | 1.095 |

Table 1-23: Estimates and 95% confidence intervals (CI) from the best supported model predicting *Myotis sodalis* (Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | β | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 2.837 | 0.717 | 4.957 |
| Date | -0.470 | -0.766 | -0.174 |
| Date$^2$ | -0.017 | -0.150 | 0.116 |
| Date$^3$ | 0.344 | 0.211 | 0.477 |
| Year 2017 | -0.429 | -0.729 | -0.129 |
| Avg. Temp | 0.715 | 0.525 | 0.906 |
| Δ Avg. Temp | -0.207 | -0.344 | -0.070 |
| Avg. Wind | -0.715 | -0.939 | -0.491 |
| Δ Mean. Wind | -0.007 | -0.183 | 0.169 |
| Δ Binary Precipitation | -0.157 | -0.429 | 0.116 |
| Distal Sites | -3.731 | -6.004 | -1.458 |
| Date*Avg. Temp | -0.581 | -0.743 | -0.419 |

Table 1-24: Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Myotis sodalis* (Indiana bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

| Variable | $\beta$ | Lower CI | Upper CI |
|---|---|---|---|
| (Intercept) | 2.8309 | 0.82468 | 4.83712 |
| Date | -0.5601 | -0.937 | -0.1833 |
| Date$^2$ | -0.0269 | -0.1612 | 0.10736 |
| Date$^3$ | 0.34769 | 0.21436 | 0.48101 |
| Year 2017 | -0.4052 | -0.7103 | -0.1 |
| Avg. Temp | 0.72747 | 0.53136 | 0.92358 |
| $\Delta$ Avg. Temp | -0.1996 | -0.3368 | -0.0625 |
| Avg. Wind | -0.7066 | -0.9311 | -0.4821 |
| $\Delta$ Mean. Wind | -0.007 | -0.1826 | 0.1687 |
| $\Delta$ Binary Precipitation | -0.1678 | -0.4397 | 0.10399 |
| Distance to Cave1km | -3.6278 | -6.0776 | -1.1781 |
| Distance to Cave2km | -4.7873 | -7.32 | -2.2547 |
| Distance to Cave3km | -3.0637 | -5.4182 | -0.7092 |
| Date*Distance to Cave1km | 0.15988 | -0.1897 | 0.5095 |
| Date*Distance to Cave2km | 0.2928 | -0.093 | 0.67856 |
| Date*Distance to Cave3km | -0.0572 | -0.389 | 0.27464 |
| Date*Avg. Temp | -0.5733 | -0.738 | -0.4085 |
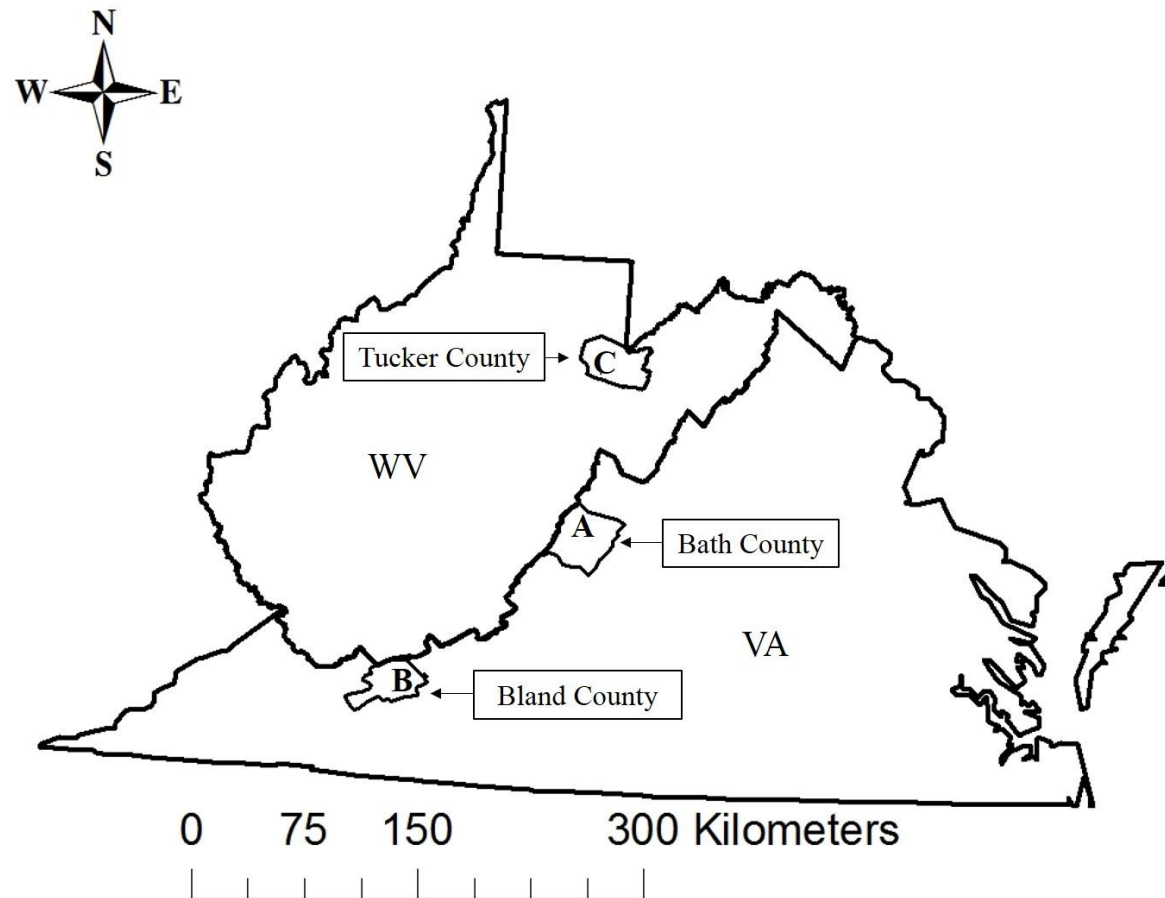
Figure 1-1: Approximate locations of caves acoustic sampling was conducted for bat species during autumn 2015 and 2016 and spring 2016 and 2017; two are located in the Ridge and Valley physiographic sub-province the central Appalachians of Virginia (A and B), and the third is in the unglaciated central Appalachian Plateau physiographic sub-province of West Virginia (C).
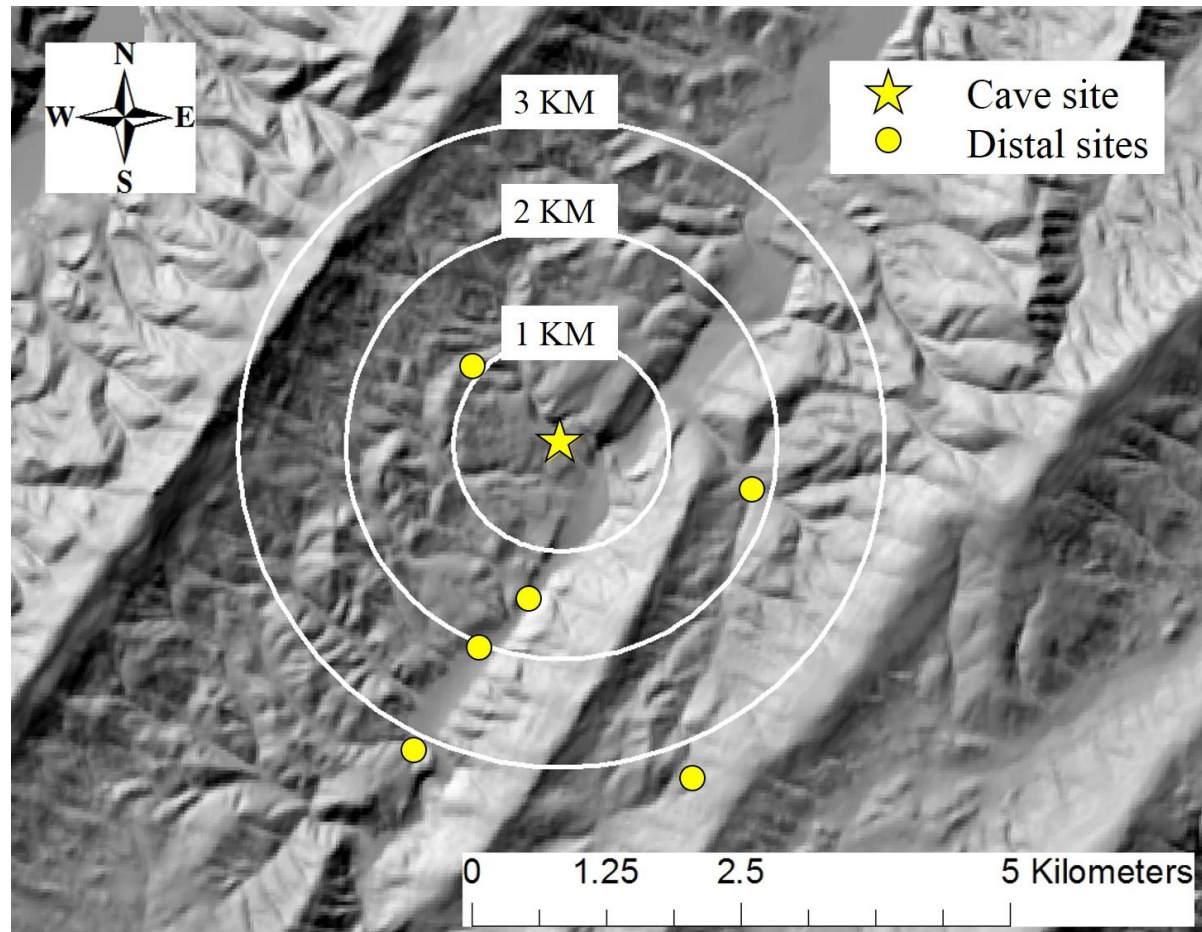
Figure 1-2: Example of acoustic sampling setup around cave sites. Acoustic detector locations were chosen based on land ownership, access, and proximity to the 'km rings', in habitats where *Myotis sodalis* (Indiana bat) and *Myotis septentrionalis* (northern long-eared bat) presence was likely, and where habitat physical features supported high-quality recordings. Acoustic detectors were deployed in this manner around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016 and spring 2016 and 2017.
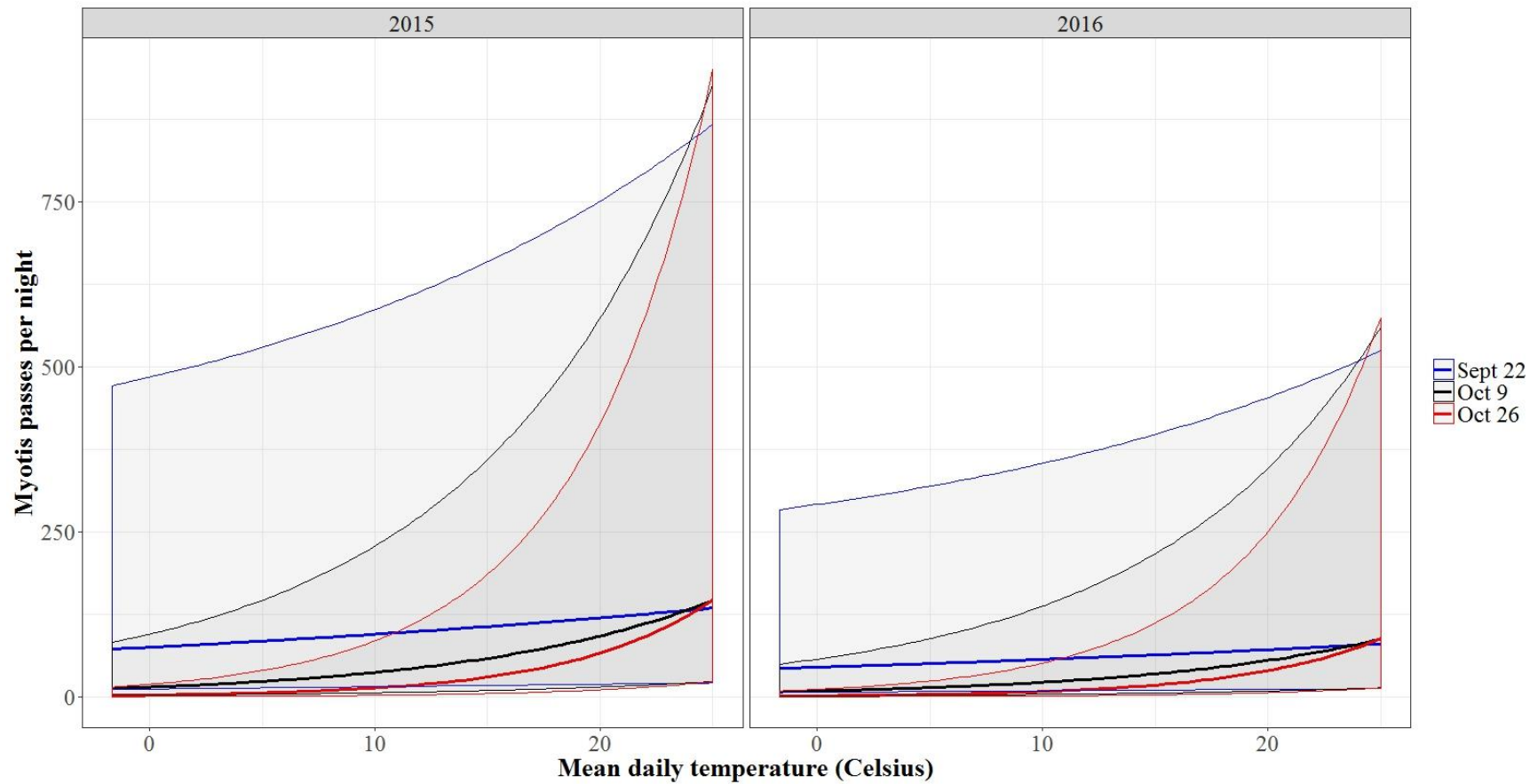
Figure 1-3: Partial effects plot of the interacting relationship between mean daily temperatures, date, and *Myotis* species' (*Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat) echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. Panels show differences in number of passes between sampling years. Predicted activity from an early- (blue), mid-(black), and late-season (red) date are shown.
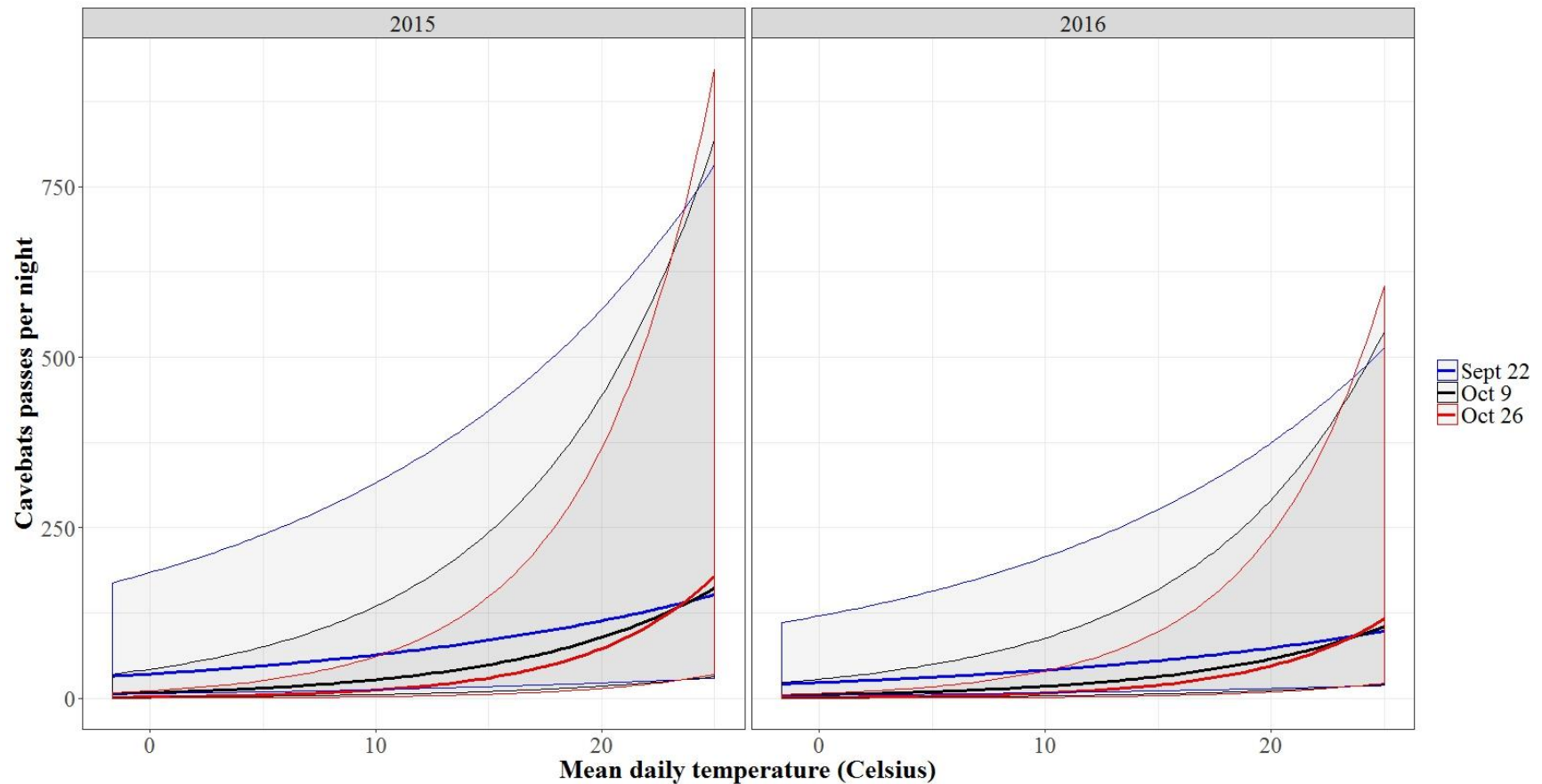
Figure 1-4: Partial effects plot of the interacting relationship between mean daily temperatures, date and 'cavebat' species' (*Eptesicus fuscus*, big brown bat; *Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat; *Perimyotis subflavus*, eastern tricolored bat) echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. Panels show differences in number of passes between sampling years. Predicted activity from an early- (blue), mid-(black), and late-season (red) date are shown.
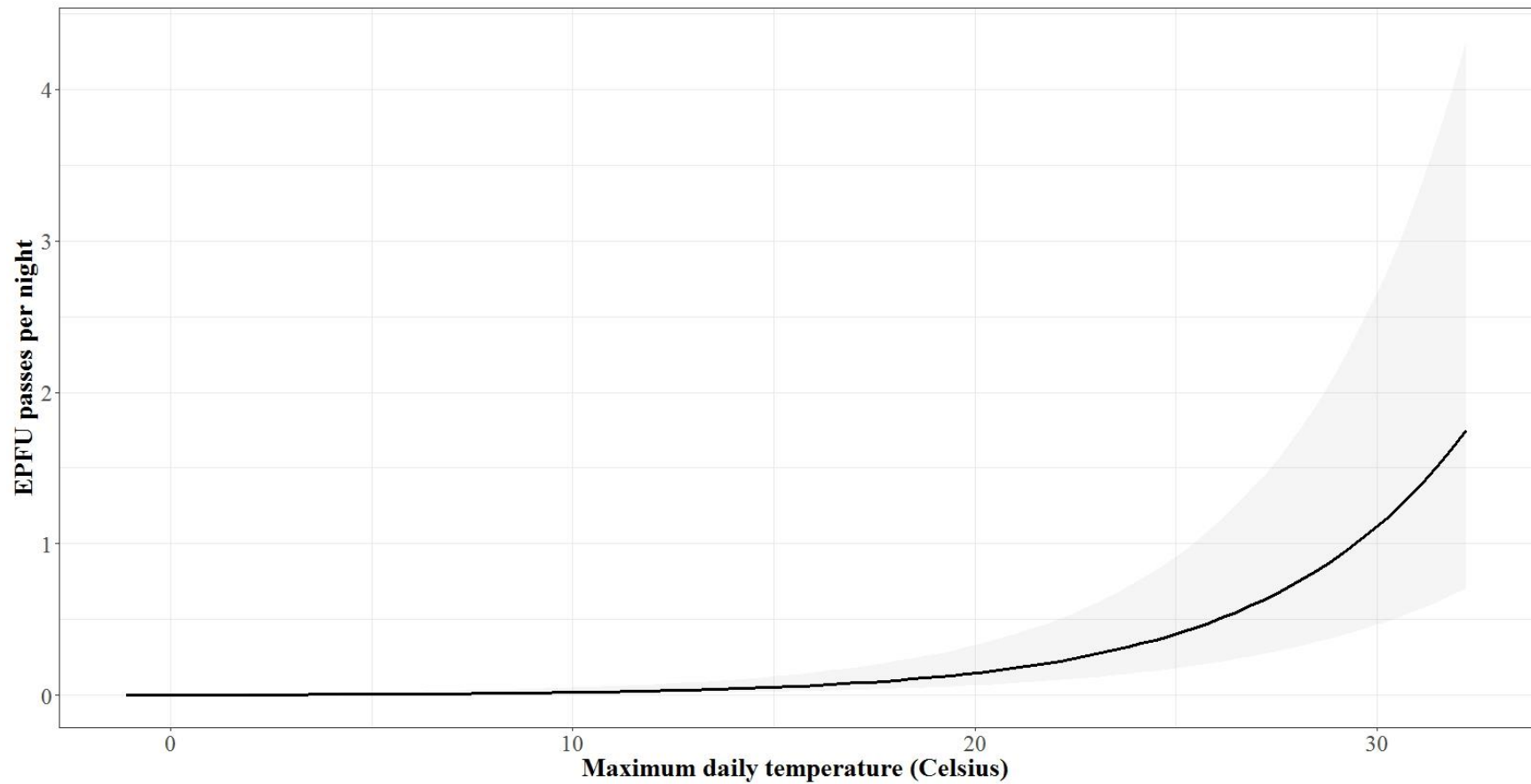
Figure 1-5: Partial effects plot of the relationship between maximum daily temperature and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.
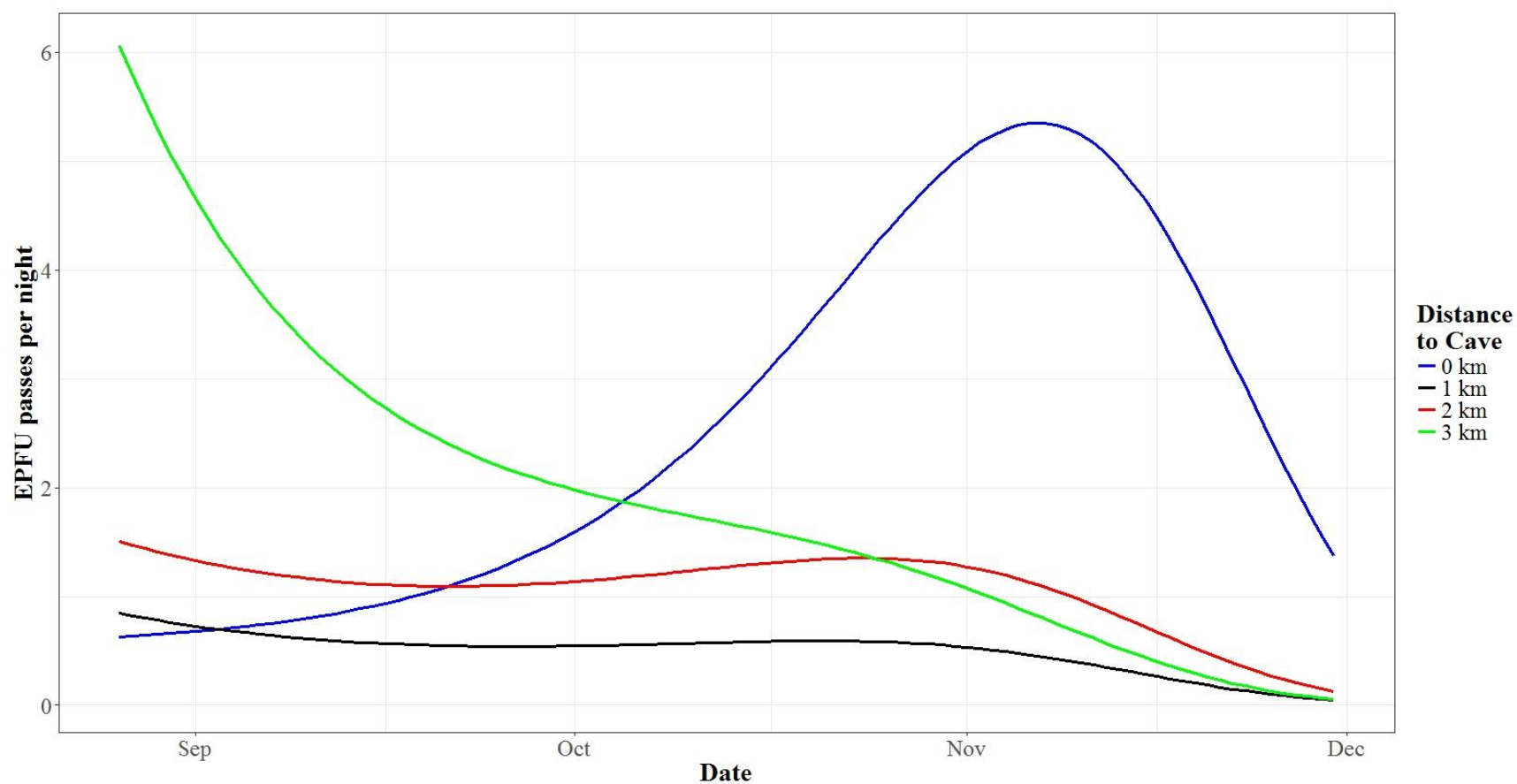
Figure 6: Partial effects plot of the interacting relationship between date, distance to hibernacula and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. Confidence intervals not shown for clarity.
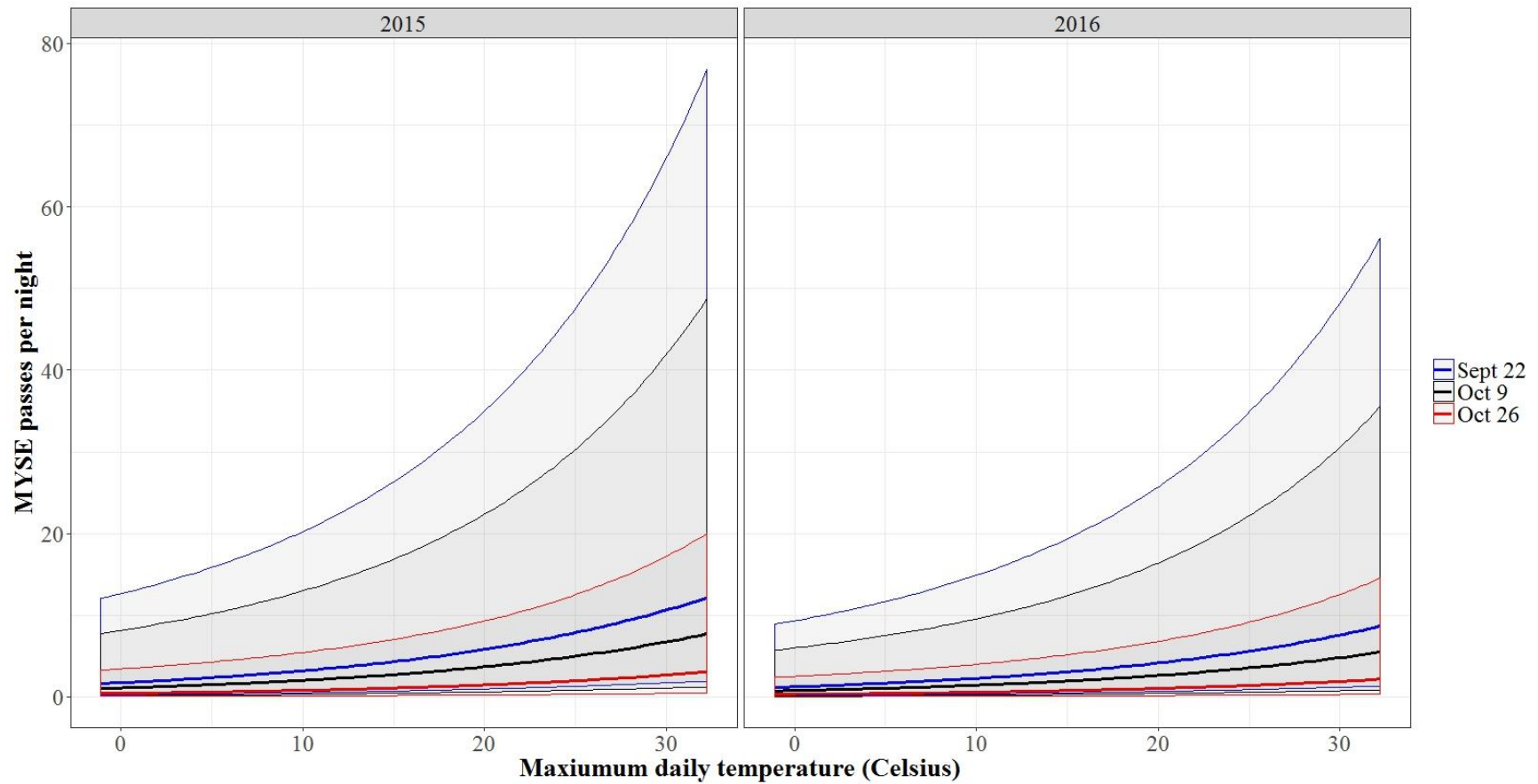
Figure 1-7: Partial effects plot of the relationship between maximum daily temperatures, date and northern long-eared bat, *Myotis septentrionalis*, northern long-eared bat (MYSE), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. Panels show differences in number of passes between sampling years. Predicted activity from an early- (blue), mid-(black), and late-season (red) date are shown.
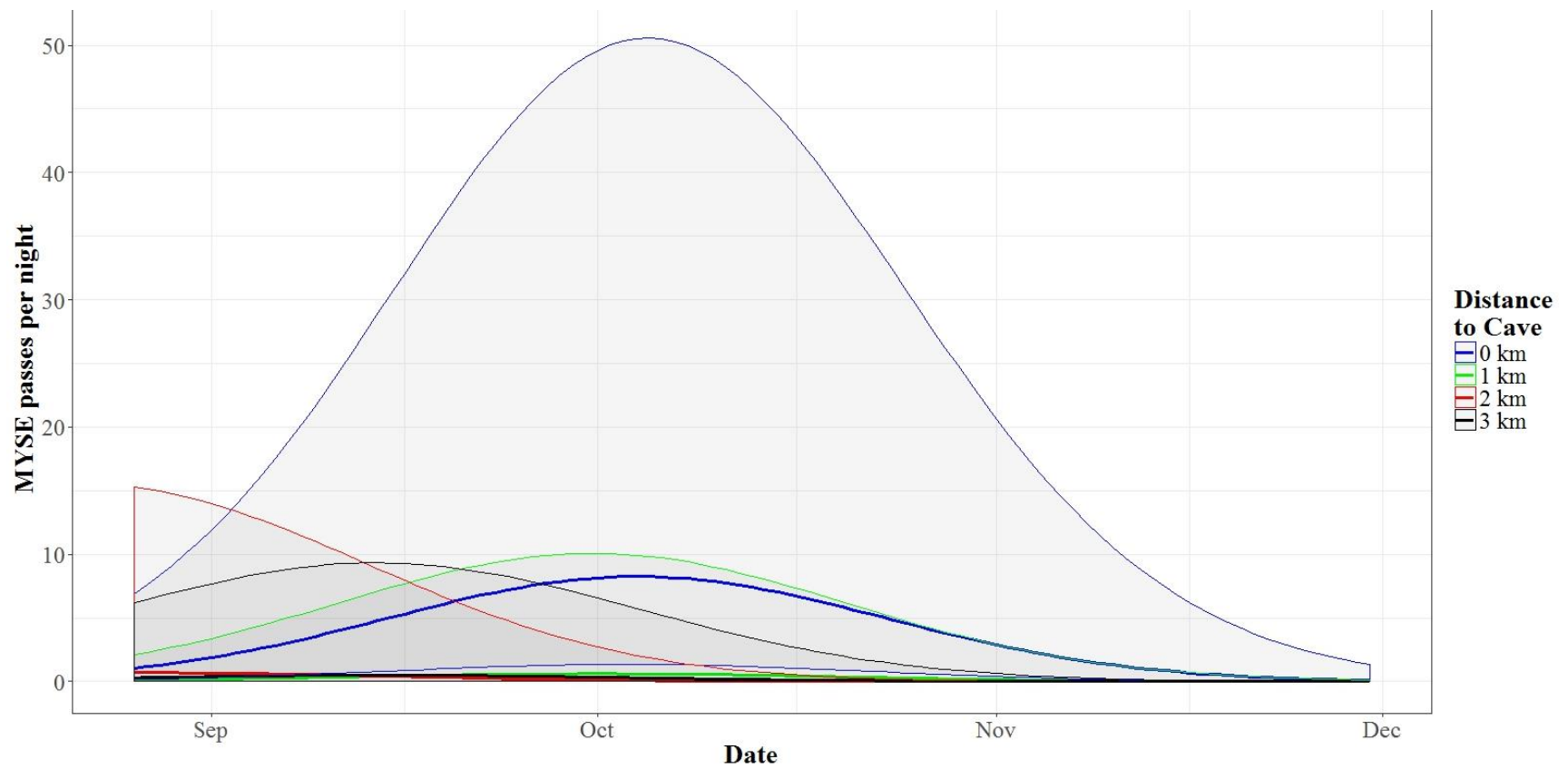
Figure 1-8: Partial effects plot of the relationship between date, distance to hibernacula, and *Myotis septentrionalis*, northern long-eared bat (MYSE), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.
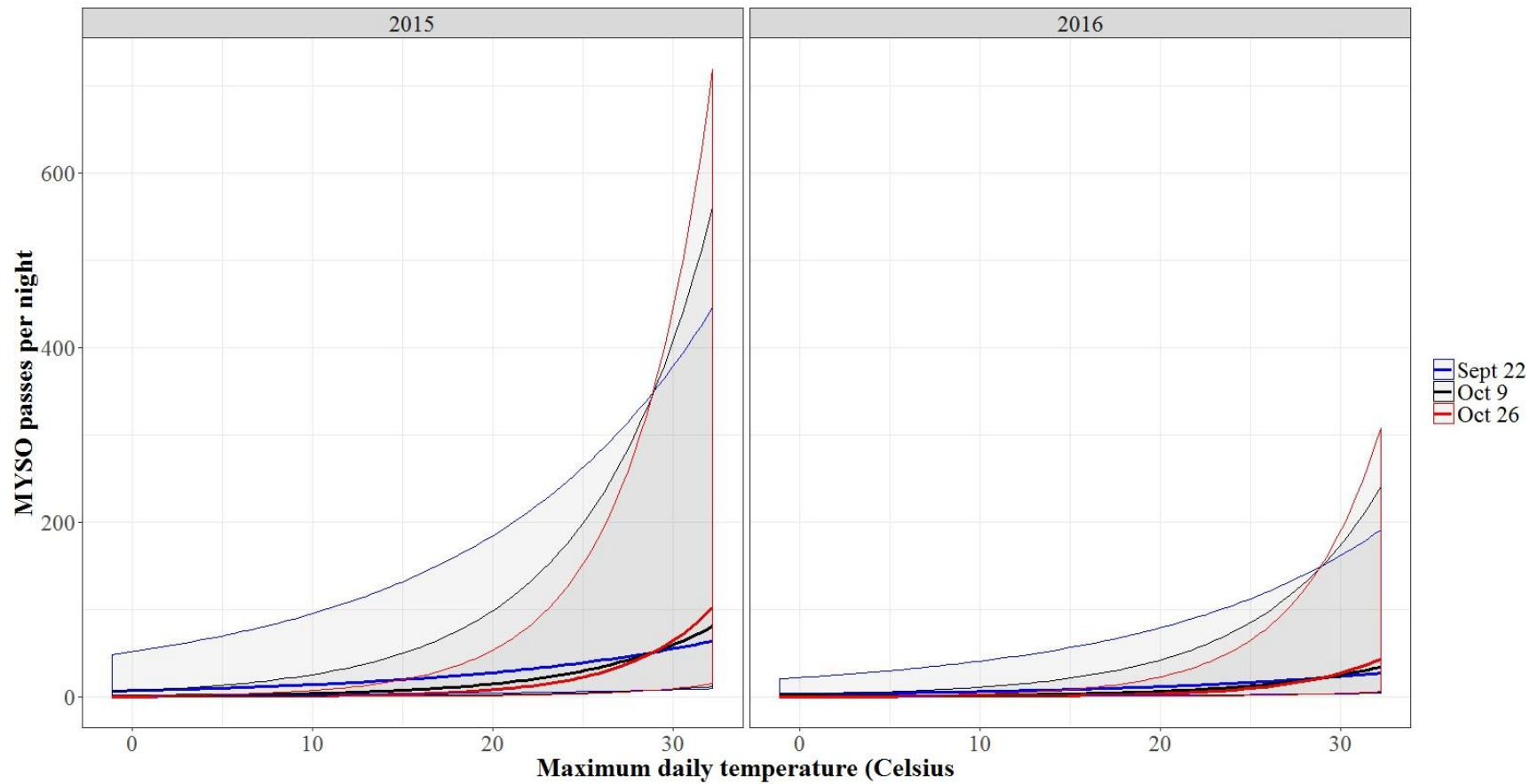
Figure 1-9:  Partial effects plot of the interacting relationship between maximum daily temperatures, date, and *Myotis sodalis*, Indiana bat (MYSO), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. Panels show differences in number of passes between sampling years. Predicted activity from an early- (blue), mid-(black), and late-season (red) date are shown.
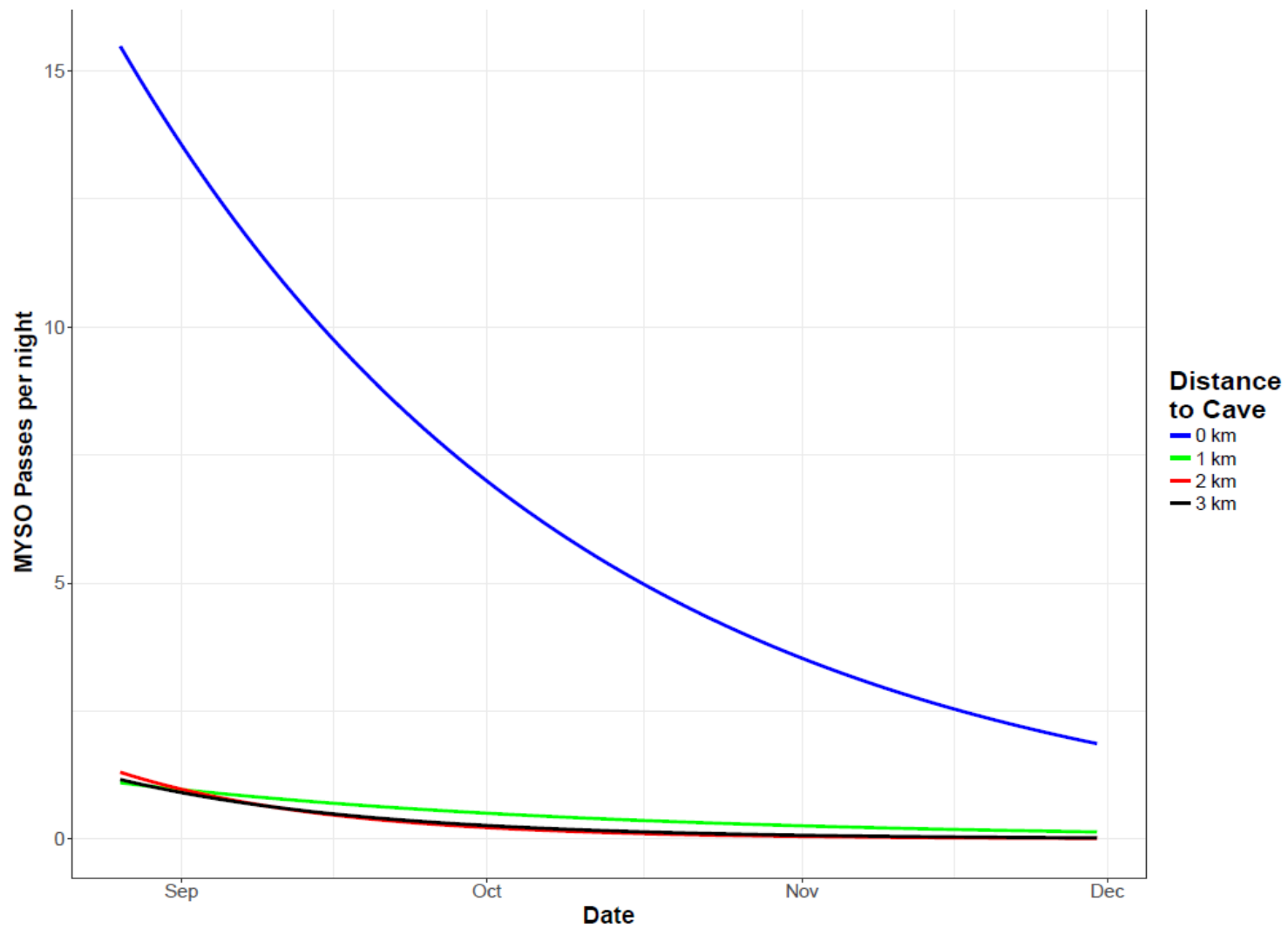
Figure 1-10: Partial effects plot of the relationship between date, distance to hibernacula and *Myotis sodalis*, Indiana bat (MYSO), echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. Confidence intervals not shown for clarity.
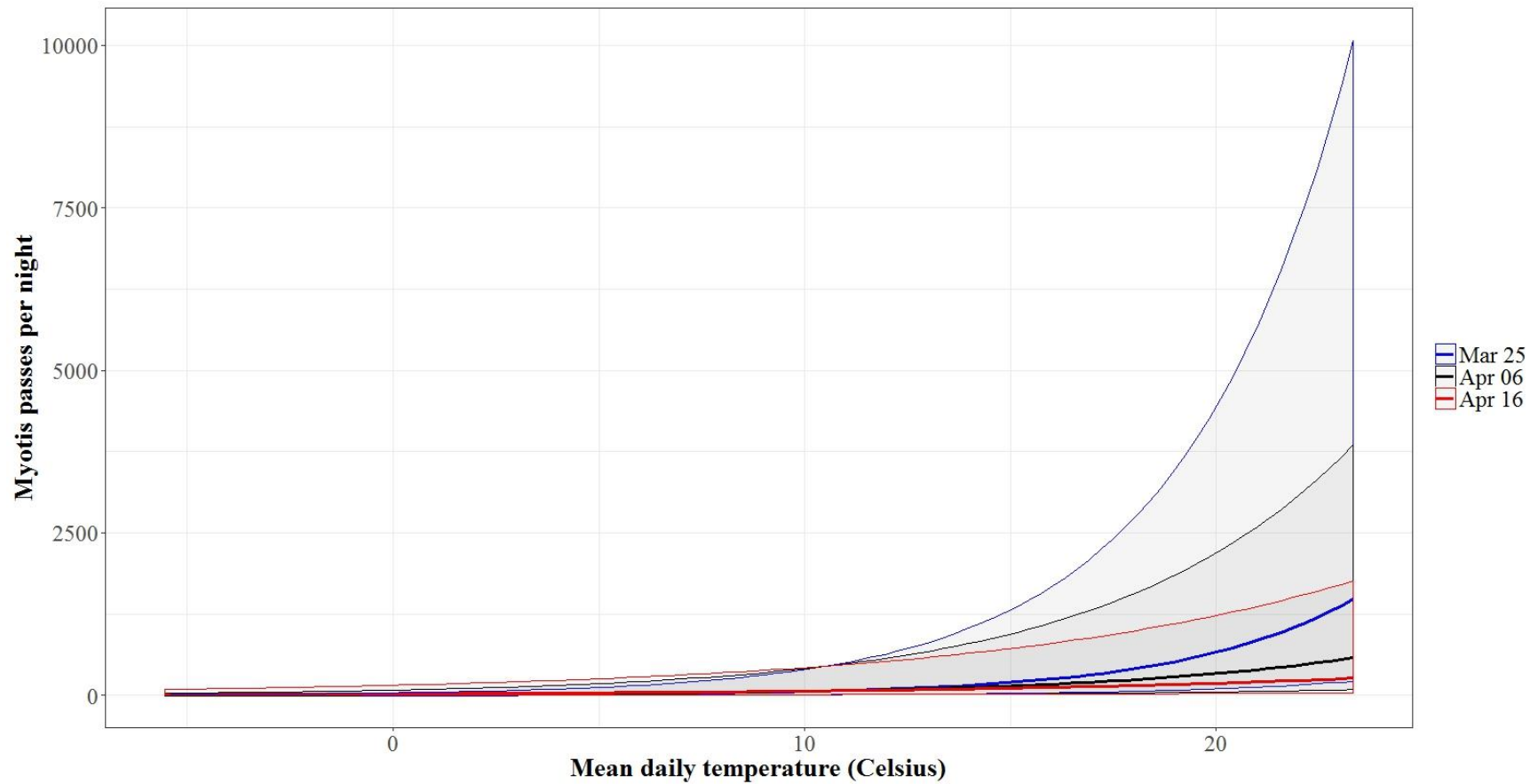
Figure 1-11: Partial effects plot of the relationship between mean daily temperatures, date, and *Myotis* species' (*Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat) echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. Predicted activity from an early- (blue), mid-(black), and late-season (red) date are shown.
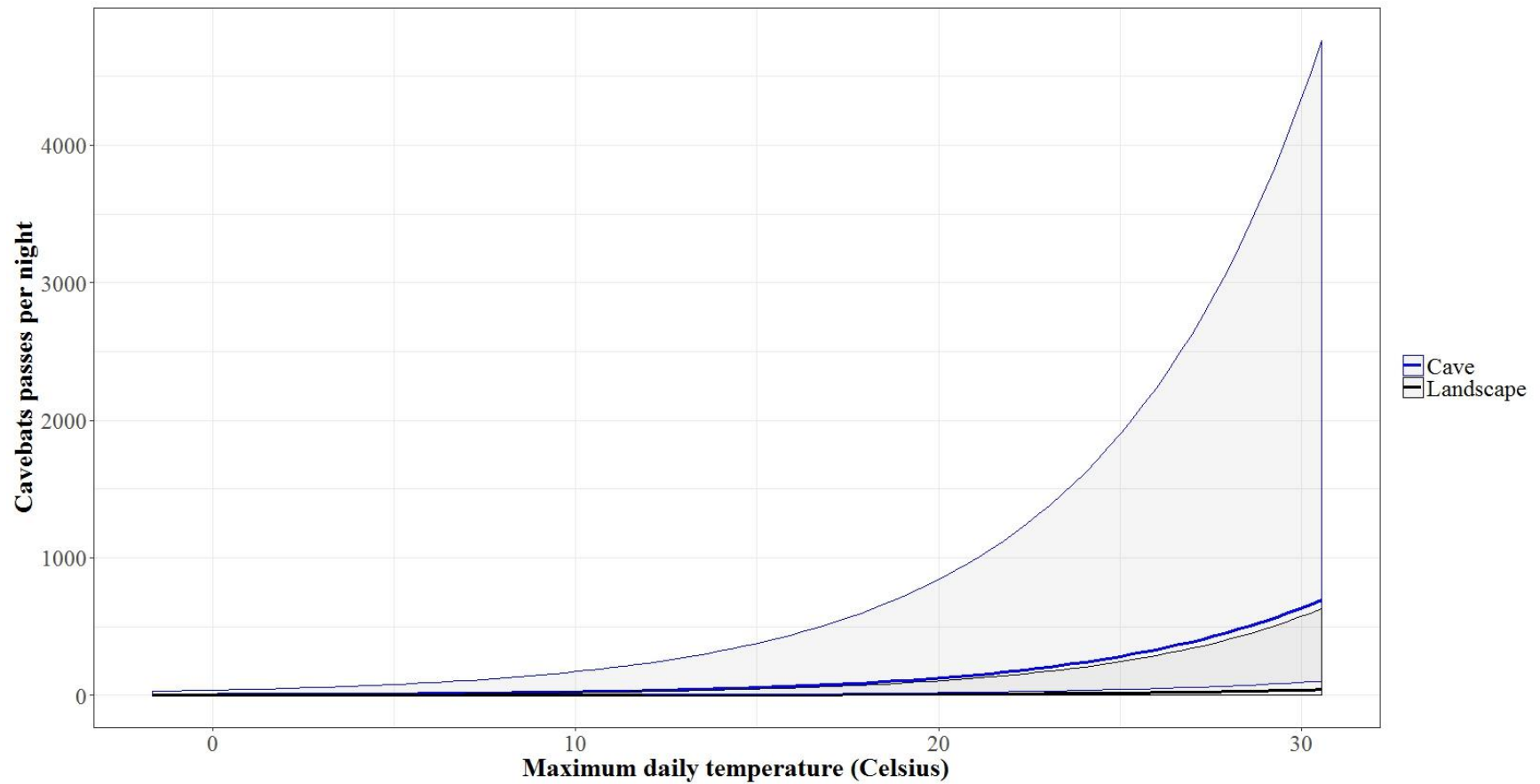
Figure 1-12: Partial effects plot of the relationship between maximum daily temperatures, proximity to caves, and 'cavebat' species' (*Eptesicus fuscus*, big brown bat; *Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat; *Perimyotis subflavus*, eastern tricolored bat) echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. Predicted activity from sample sites proximal to cave entrances (blue), and distal sites up to 3 km away from cave entrances (black) are shown.
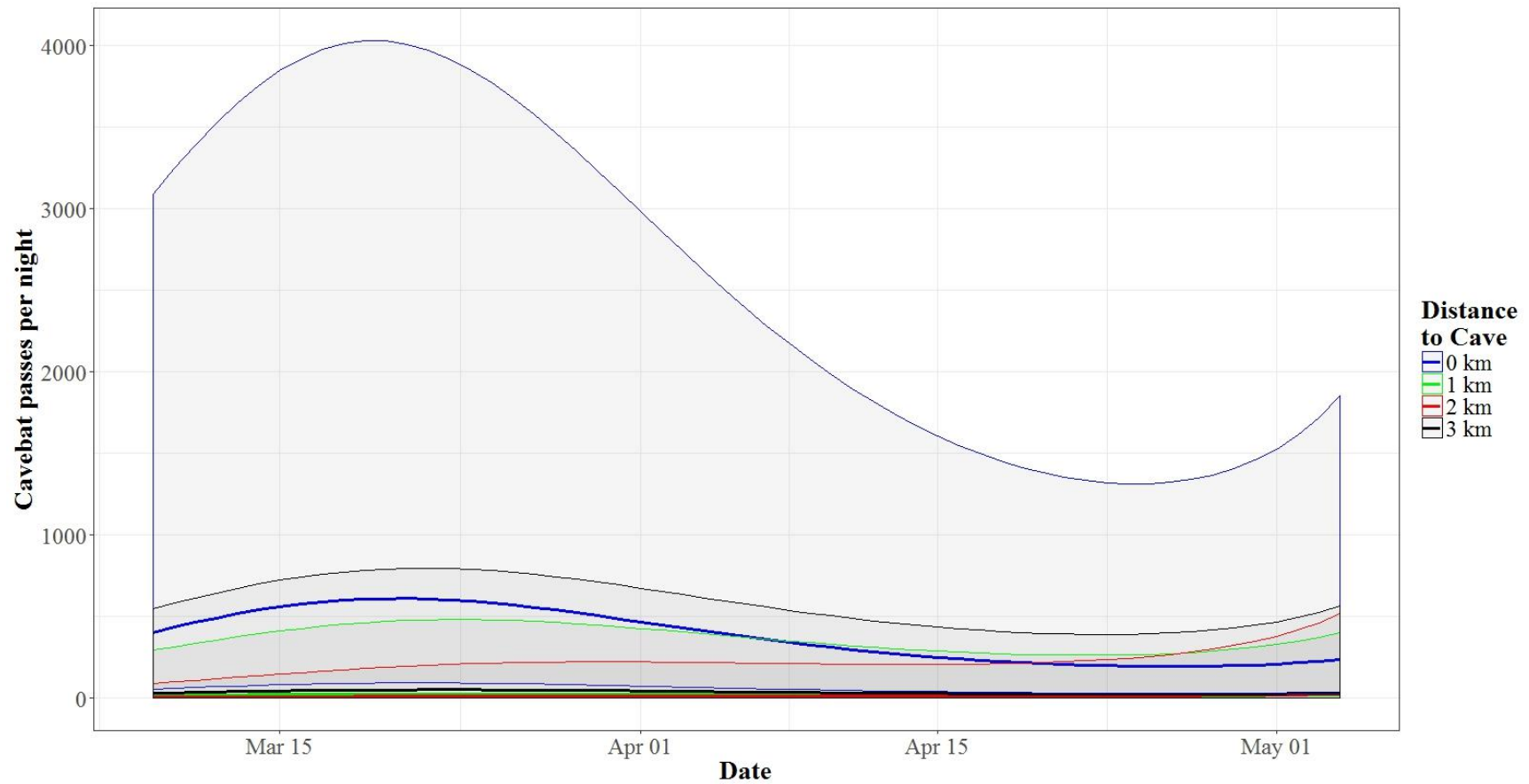
Figure 1-13: Partial effects plot of the relationship between date, distance to cave, and 'cavebat' species' (*Eptesicus fuscus*, big brown bat; *Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat; *Perimyotis subflavus*, eastern tricolored bat) echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017.
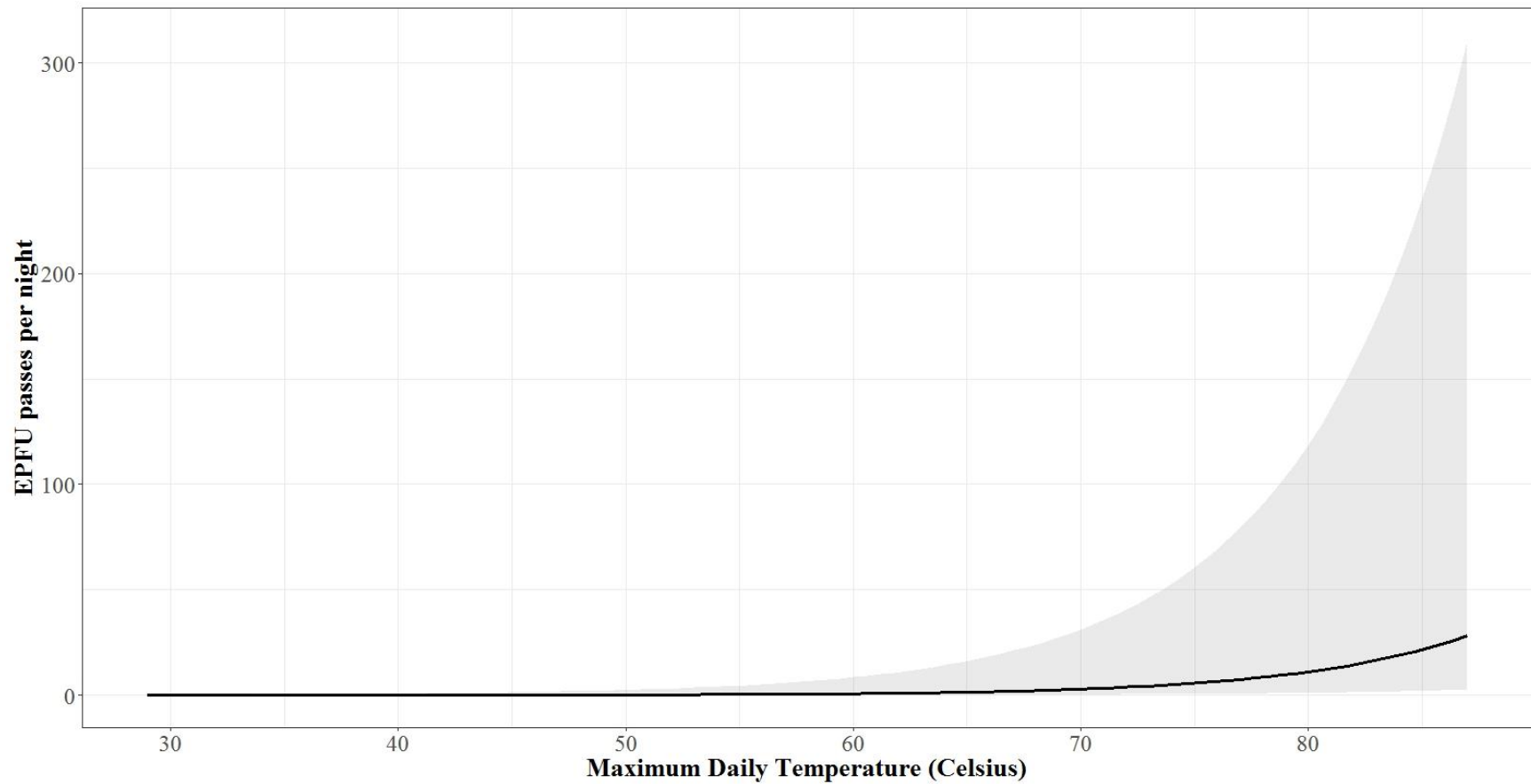
Figure 1-14: Partial effects plots of the relationship between maximum daily temperatures and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017.
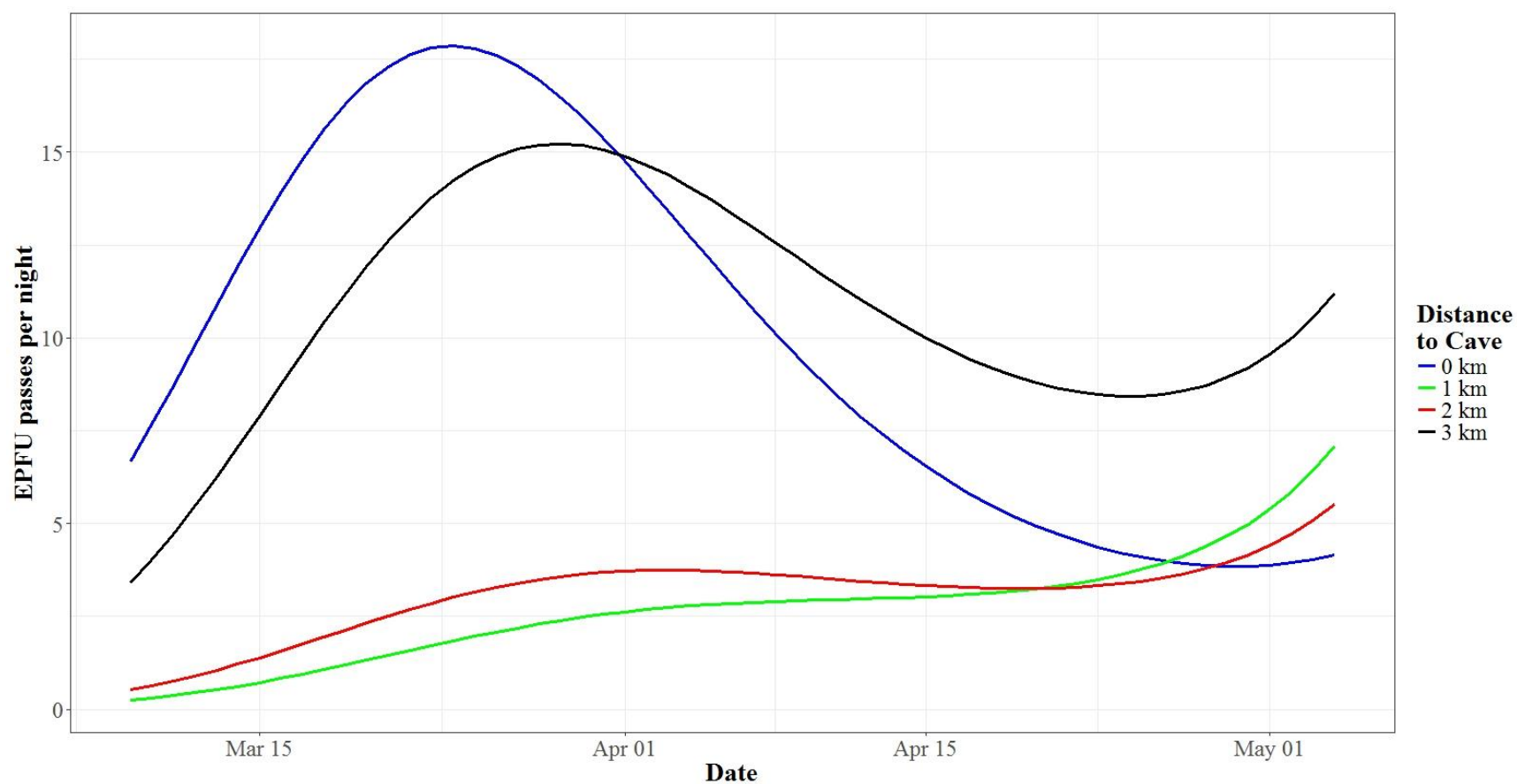
Figure 1-15: Partial effects plot of the interacting relationship between date, distance to cave, and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. Confidence intervals not shown for clarity. The EPFU relative activity increased at distal sites faster than at cave sites later in the spring.
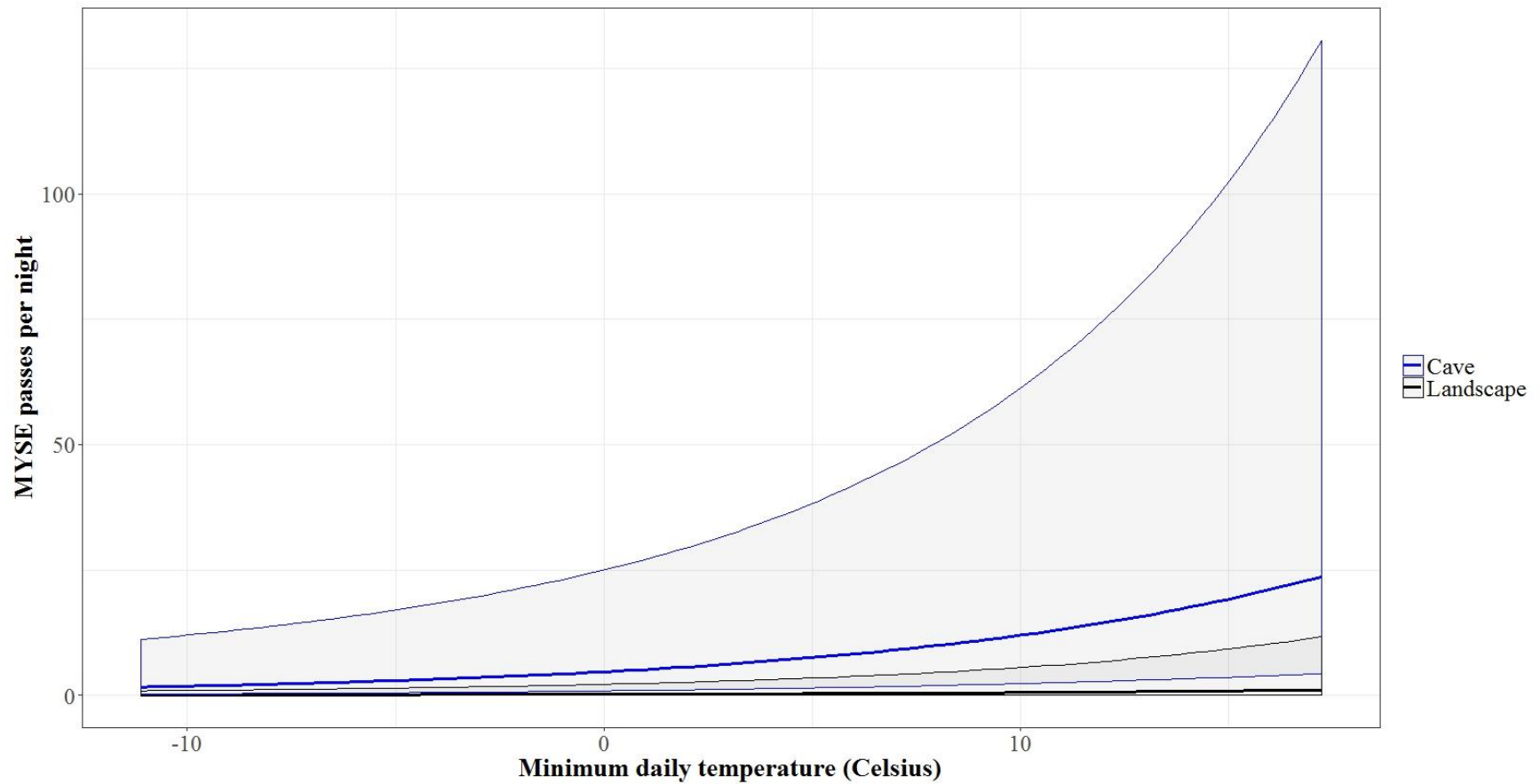
Figure 1-16: Partial effects plot of the relationship between minimum daily temperatures, proximity to cave, and *Myotis septentrionalis*, northern long-eared bat (MYSE), echolocation passes per night (with 95% confidence interval) around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. Predicted activity from sample sites proximal to cave entrances (blue), and distal sites up to 3 km away from cave entrances (black) are shown.
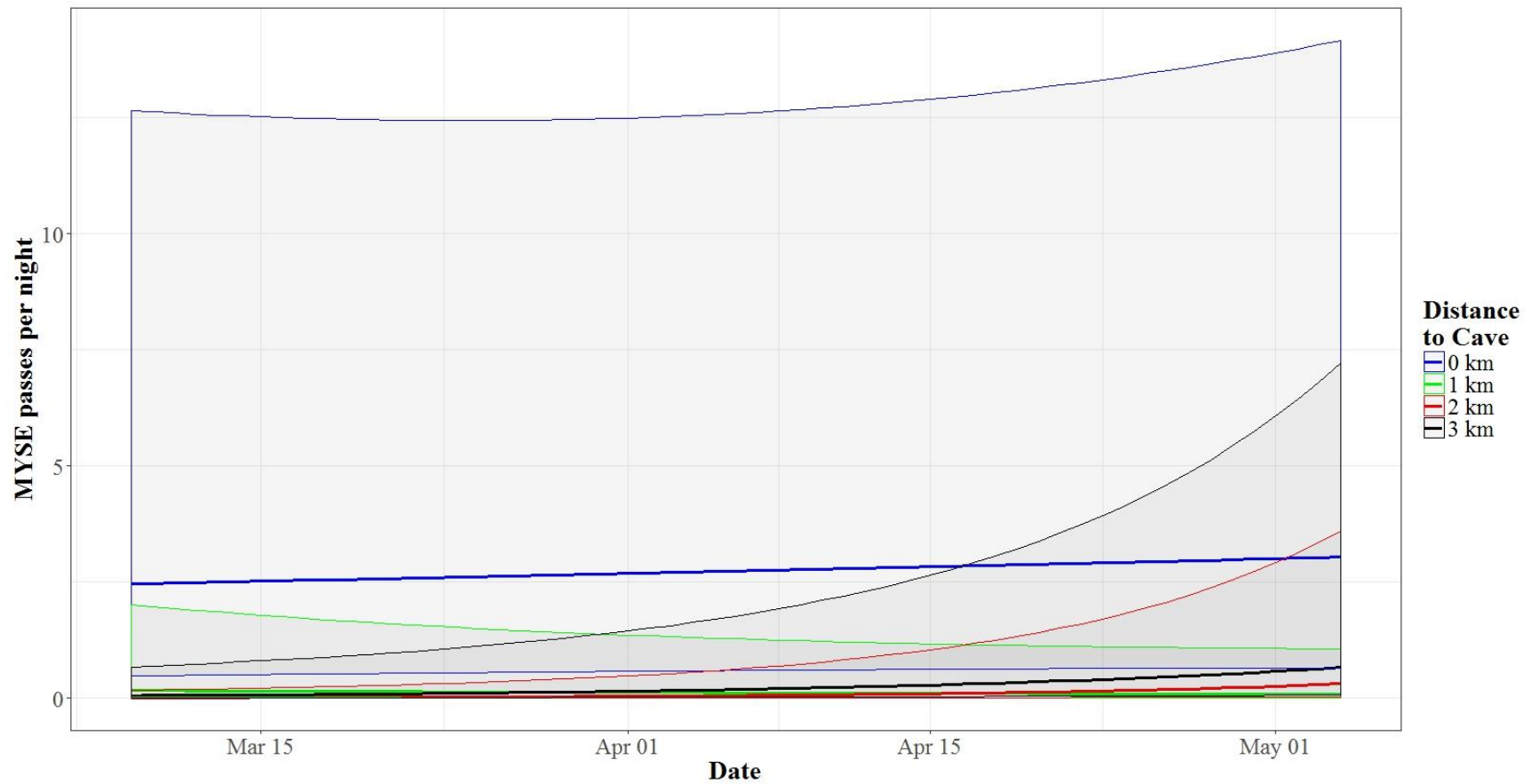
Figure 1-17: Partial effects plot of the interactive relationship between date, distance to cave, and *Myotis septentrionalis*, northern long-eared bat (MYSE), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017.
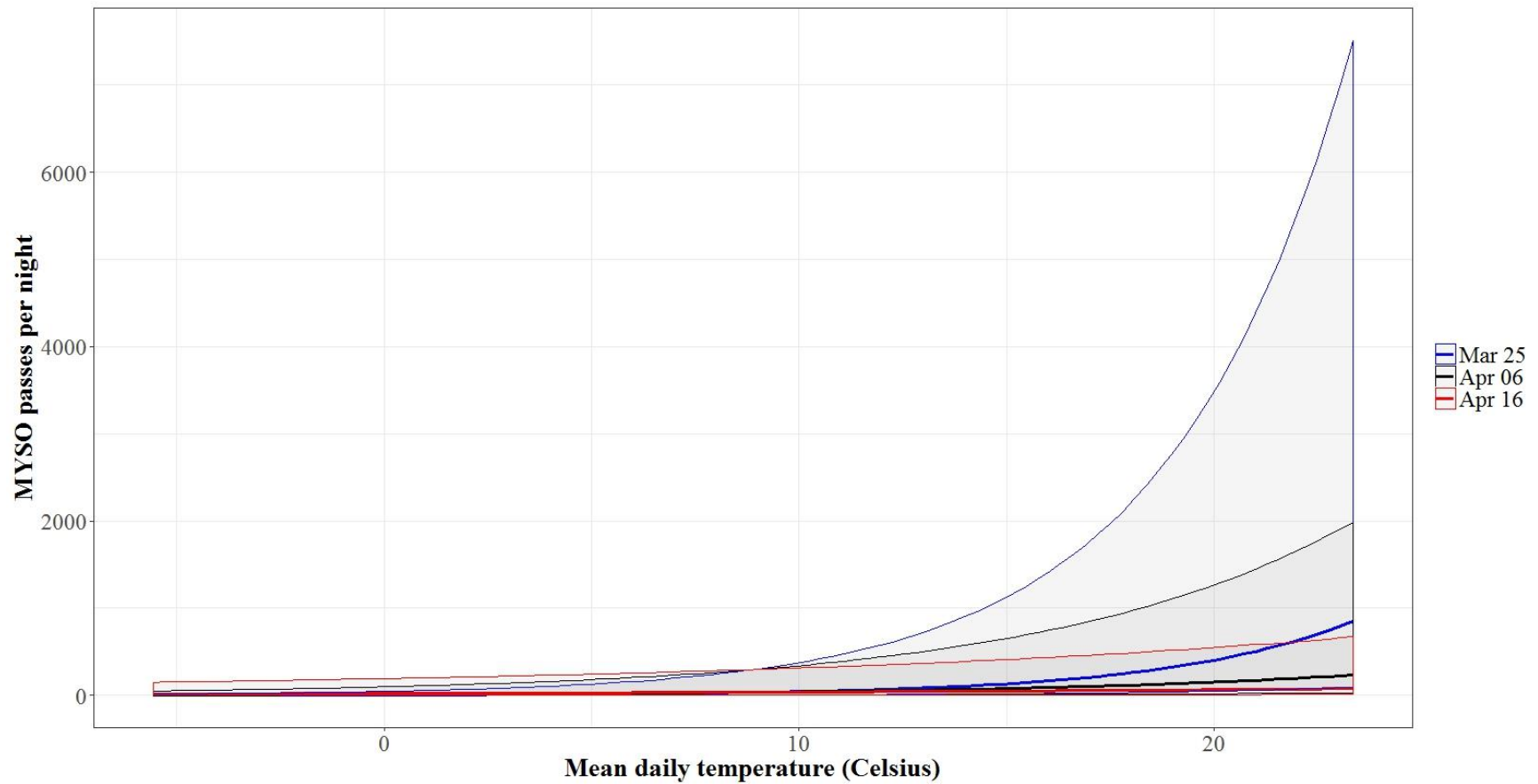
Figure 1-18: Partial effects plot of the relationship between mean daily temperature, date, and *Myotis sodalis*, Indiana bat (MYSO), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. Predicted activity from an early- (blue), mid-(black), and late-season (red) date are shown.
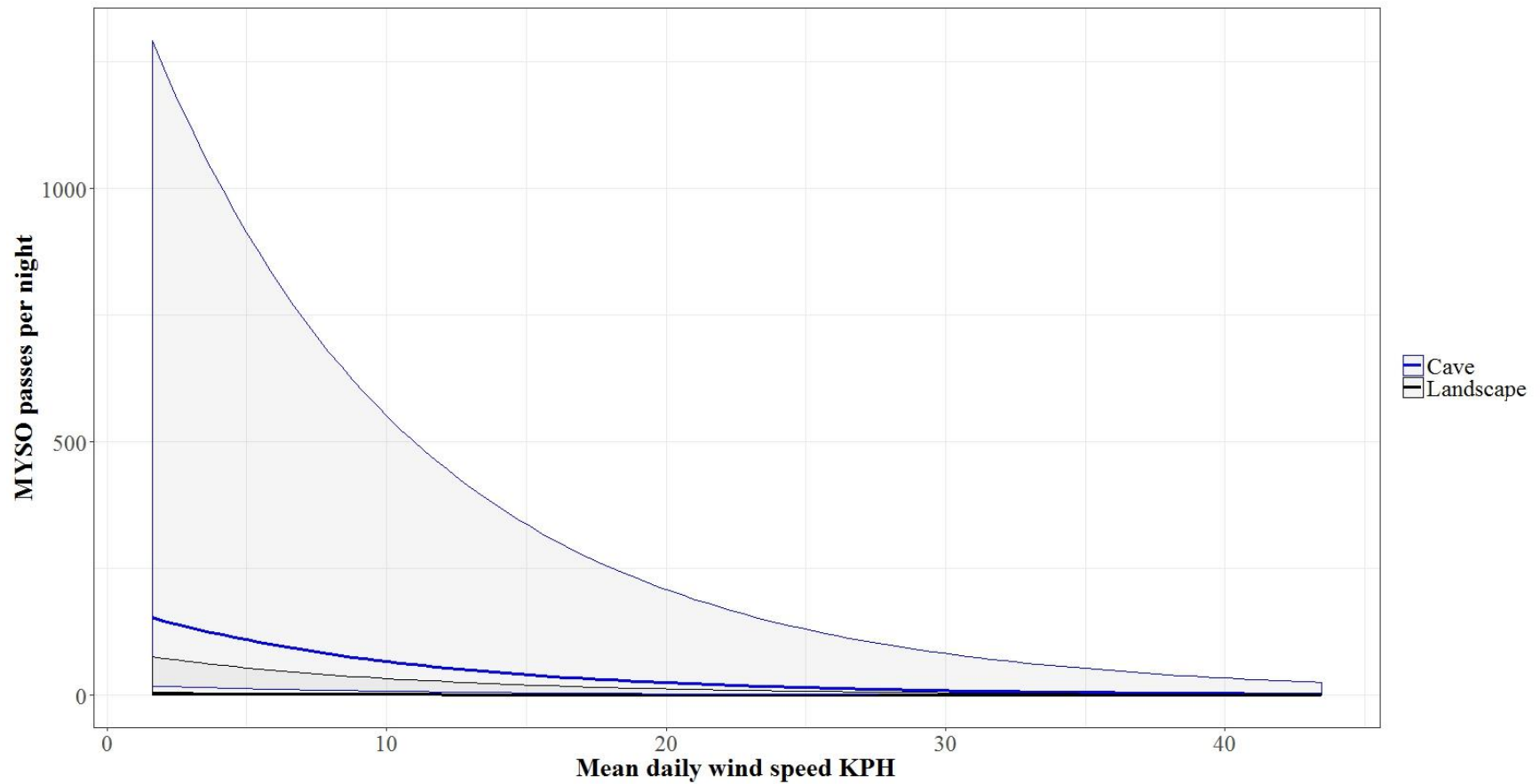
Figure 1-19: Partial effects plot of the relationship between mean daily wind speed, proximity to cave, and *Myotis sodalis*, Indiana bat (MYSO), echolocation passes per night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. Predicted activity from sample sites proximal to cave entrances (blue), and distal sites up to 3 km away from cave entrances (black) are shown.
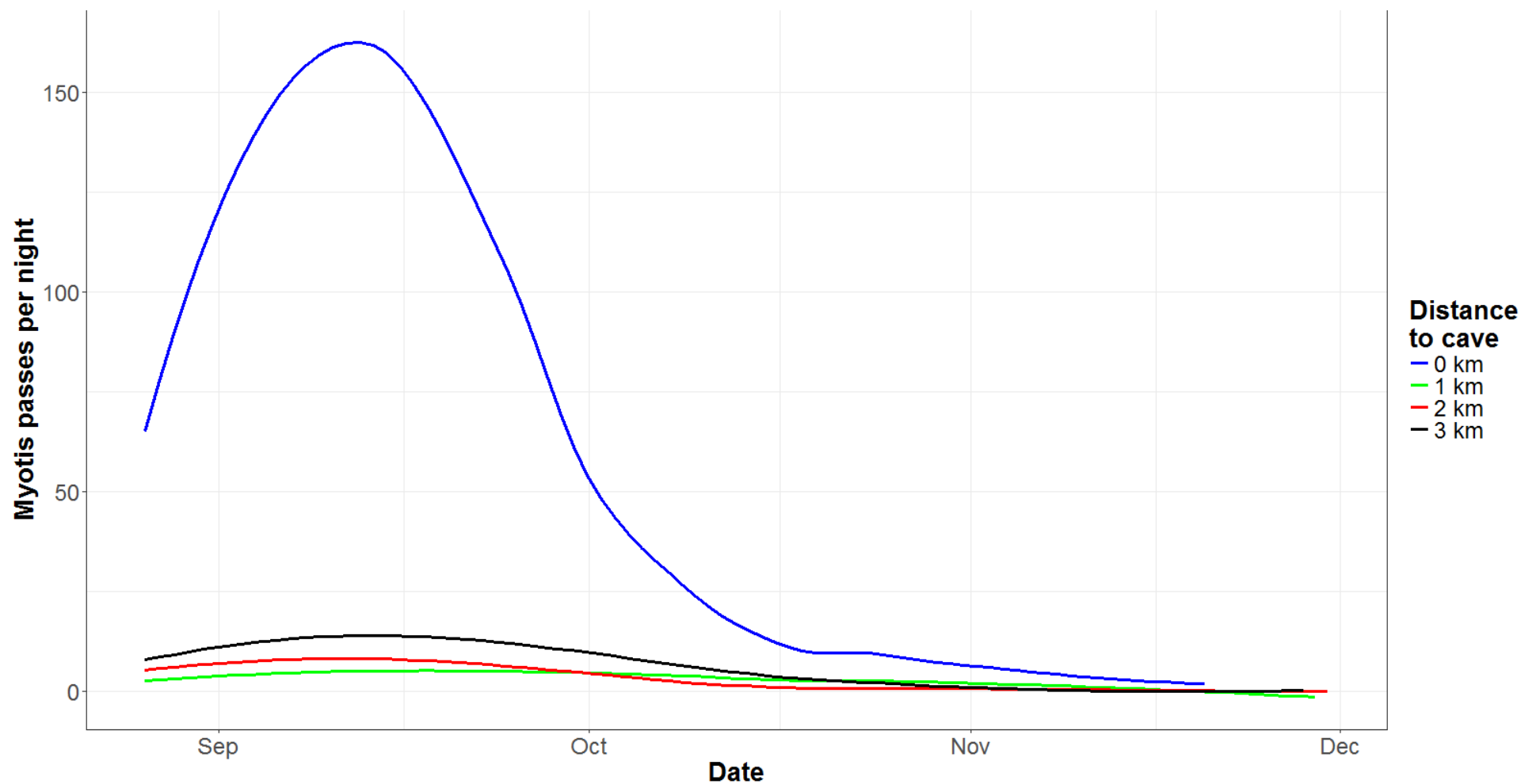
Figure 1-20: Smoothed trend line of raw data showing general timing of *Myotis* species' (*Myotis leibii,* eastern small-footed bat; *Myotis lucifugus,* little brown bat; *Myotis septentrionalis,* northern long-eared bat; *Myotis sodalis,* Indiana bat) echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.
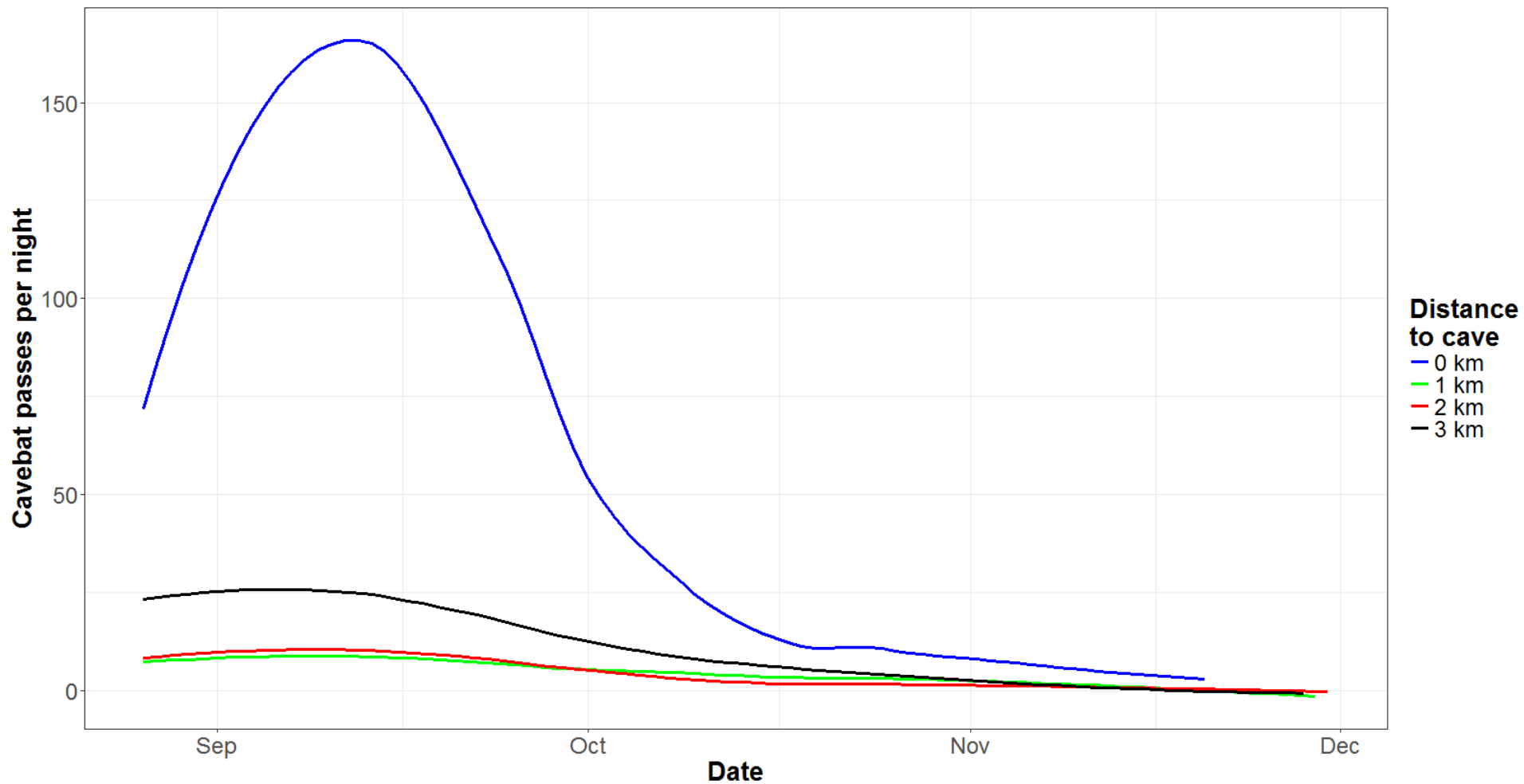
Figure 1-21: Smoothed trend line of raw data showing general timing of 'cavebat' species' (*Eptesicus fuscus*, big brown bat; *Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat; *Perimyotis subflavus*, eastern tricolored bat) echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.
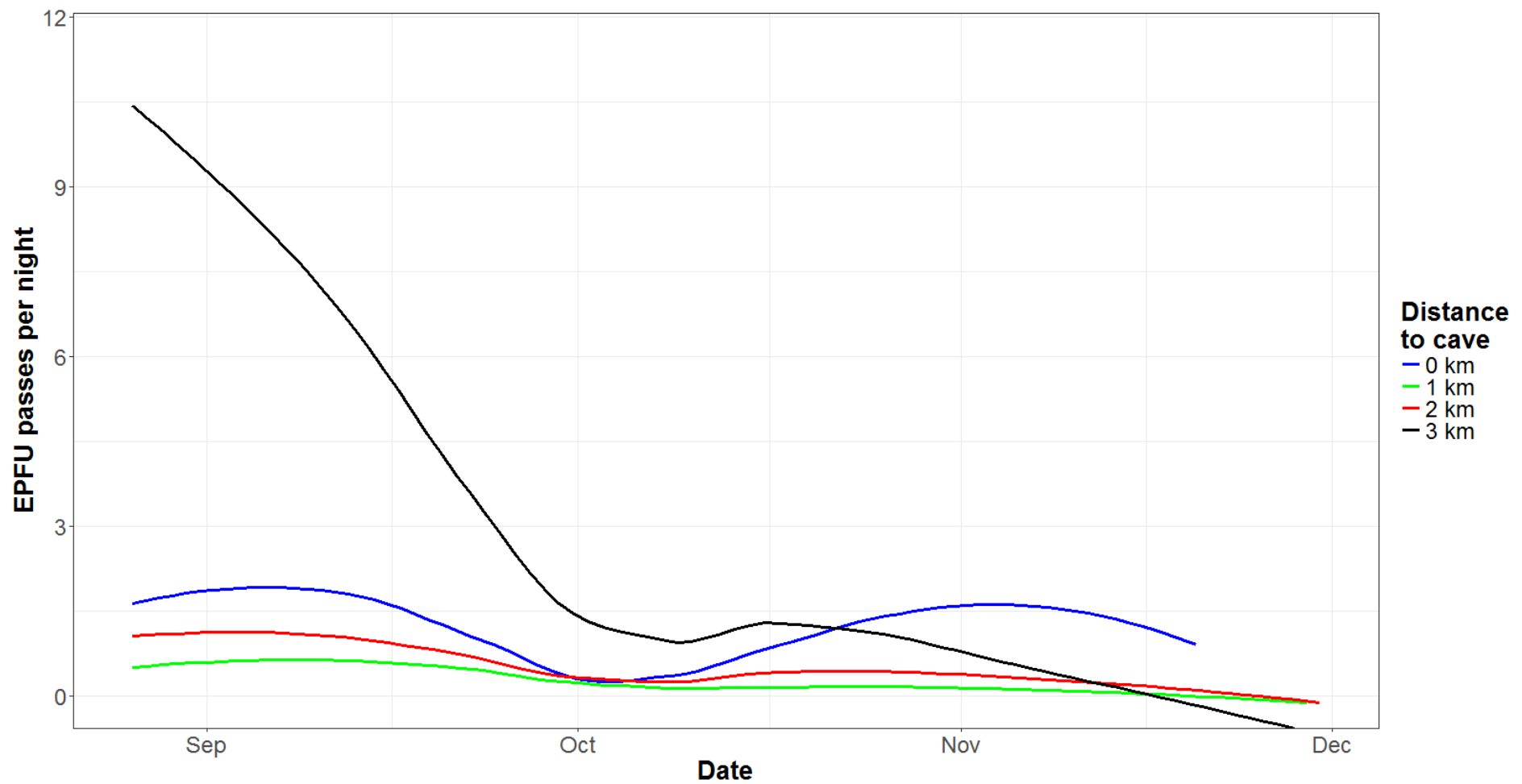
Figure 1-22: Smoothed trend line of raw data showing general timing of *Eptesicus fuscus,* big brown bat (EPFU), echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016. Confidence intervals not shown for clarity.
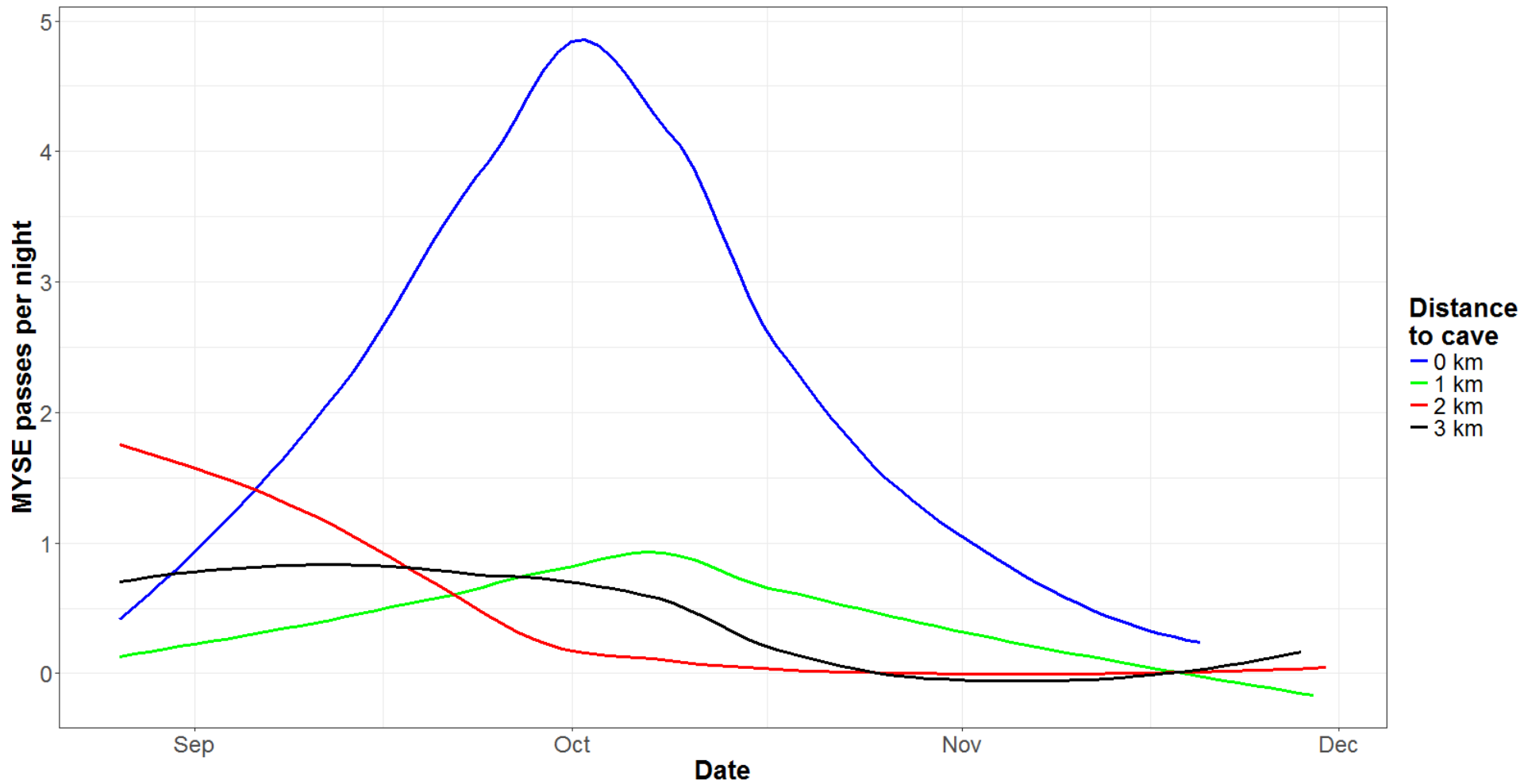
Figure 1-23: Smoothed trend line of raw data showing general timing of *Myotis septentrionalis*, northern long-eared bat (MYSE), echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.
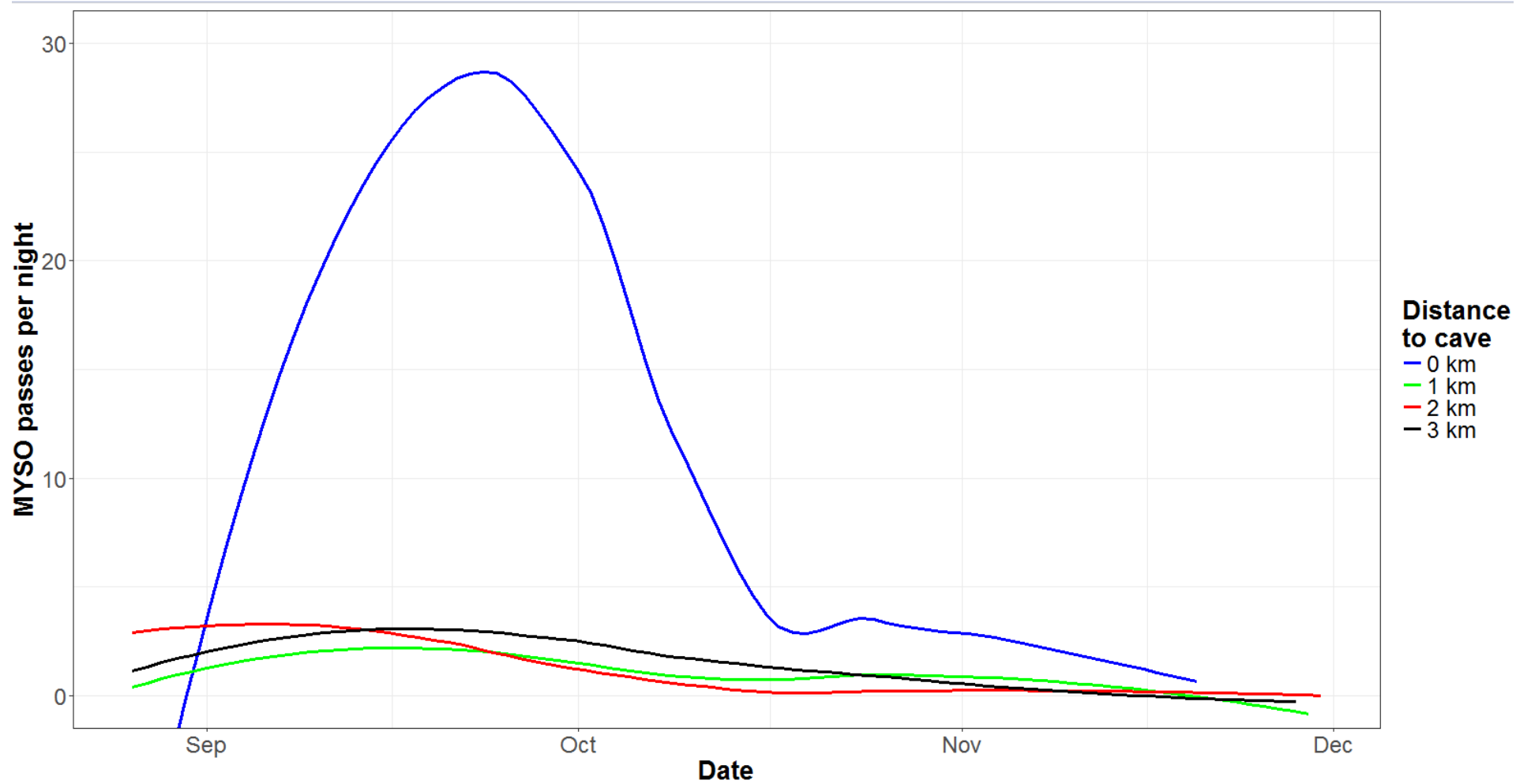
Figure 1-24: Smoothed trend line of raw data showing general timing of *Myotis sodalis*, Indiana bat (MYSO), echolocation passes per night around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016.

*Chapter 2: Activity patterns in regional and long-distance migrant bat species during the fall and spring along ridgelines in the central Appalachians.*

*Abstract*

Although considered a carbon-neutral, clean energy form, wind energy has been shown to have substantial negative impacts on bat populations, particularly in the Appalachians where high bat fatality rates are reported. Many central Appalachian ridges offer high wind potential, making them attractive to future wind energy development. Understanding regional seasonal and hourly activity patterns of migratory bat species may help to reduce fatalities at existing and future wind energy facilities and provide guidance for the development of best management practices relative to bats. To examine hourly migratory bat activity patterns in the fall in Virginia, we acoustically monitored bat activity on five ridgelines and sideslopes from early September through mid-November 2015 and 2016 and from early March through late April 2016 and 2017. On ridges, overall bat activity decreased through the autumn sample period, but was more variable through the spring sample period. In autumn, migratory bat activity had largely ceased by mid-November. Activity patterns were species-specific in both autumn and spring sample periods. Generally, migratory bat activity was related negatively with hourly wind speeds but positively related with ambient temperatures. These data provide further evidence that operational mitigation strategies at wind energy facilities would help protect migratory bat species in the Appalachians; substantially slowing or stopping wind turbine blades' spin during periods of low wind speeds and warm ambient temperatures would help avoid mortality during periods of high bat activity.

*Introduction*

Although most bat species in eastern North America hibernate in caves during the winter (hereafter cave bats), the eastern red bat (*Lasiurus borealis,* LABO), hoary bat (*Lasiurus cinereus;* LACI), and silver-haired bat (*Lasionycteris noctivagans;* LANO) are migratory and day-roost in trees year round (hereafter tree bats; Barbour and Davis 1969). All three species are widespread throughout North America during summer months: LABO occur mainly east of the Continental Divide, LACI generally occur in southern Canada and in northern states, and LANO occur from southeastern Alaska south throughout Canada and northern United States. (Cryan 2003). Both LANO and LABO appear to overwinter in the southeastern United States; although less is known of LACI wintering habits, it is assumed the species follows similar migration patterns, wintering from the southeastern United Statesr as far south as Mexico and Central America (Kurta 1995). In the central Appalachians, iittle is known about the specific habits and activity of tree bats in North America during the spring and fall migration periods, when mortality from wind energy appears to be greatest (Cryan 2003). The current dearth of knowledge on tree bats can partly be attributed to the difficulty of studying these highly mobile species (Holland and Wikelski 2009).

Many studies to date address large-scale seasonal occurrence and distribution patterns, but smaller-scale, spatially-explicit activity patterns in migratory bats remain largely unexplored (Cryan 2003, Kunz and Fenton 2006). Furthermore, in the central Appalachians, some LABO can remain in the region through the winter months, roosting in leaf litter (Davis and Lidicker 1956, Cryan 2003). However, it is unknown if these LABO wintering in the central Appalachians are resident year-round or seasonal migrants supplying more northern latitudes

with their summer residents (Dunbar and Tomasi 2006). A more detailed analysis of autumn and spring LABO activity patterns in the central Appalachians could help to elucidate overall seasonal range dynamics.

Migrating bats appear to concentrate along specific travel routes that likely are associated with specific landscape features, such as mountain ridges, coastlines, and large valleys. For example in the eastern United States, the Appalachian Mountains and the Atlantic Coast are physiographic features that may affect and concentrate migratory bat activity (Fiedler 2004, Kerns and Horn 2005, Baerwald and Barclay 2009, Cryan and Barclay 2009, Hamilton 2012, Smith and McWilliams 2016). However, for the central Appalachians, it is unknown whether all or only certain ridges and valleys are important landscape features as is the case for some migratory birds (Newton et al. 2008), or if patterns are consistent between physiographic subprovinces within the region (i.e. Blue Ridge, Ridge and Valley, and Allegheny Plateau). Furthermore, if ridges and/or valleys in the central Appalachians act as migratory corridors, it remains unclear how elevation of ridges in relation to proximal valley floors (local relief) affects migratory bat activity.

Most existing migratory tree bat data have come from recent research focusing on mortality associated with wind turbines (e.g., Arnett et al. 2008, Hayes 2013, Martin et al. 2017). Extensive increases in wind energy developments across North America and especially in the Appalachians are expected in the coming decades (AWEA - American Wind Energy Association, 2016), especially as regional electricity production shifts away from coal-generated power (McIlmoil and Hansen 2010). Wind energy is the fastest-growing form of energy production in the U.S. today, and over a decade ago when still in its infancy in the region, it was

recognized as a serious threat to bat populations (Tuttle, 2004, Kunz and Fenton 2006, Navigant Consulting, Inc. 2017).

The vast majority of North American bat-associated wind turbine fatalities are LABO, LACI, and LANO, when these species are migrating (Fiedler 2004, Kunz and Fenton 2006, Arnett et al. 2008). There is a considerable degree of variation in bat fatality rates between different wind farms and between turbine sizes, yet much of this variation remains unexplained (Barclay et al. 2007). The highest rate of reported fatalities are at wind farms is in the eastern U.S., specifically in the Appalachians, and wind turbines are located along ridge tops in this region (Kunz et al. 2007, Arnett et al. 2008, Lott 2008, Hayes 2013). As more wind energy facilities are developed, it is imperative that land managers understand the relationships between migratory bats and wind energy in order to develop mitigation practices to curtail severe mortality events or in some cases potential extinction (Frick et al. 2017).

Clearly, migratory bat activity patterns are variable within seasons, between seasons, and associated photoperiods and atmospheric conditions (Cryan 2003, Baerwald and Barclay 2011, Weller and Baldwin 2012, Smith and McWilliams 2016). Autumn migratory bat activity patterns appear to be positively related with storm front passage and associated ambient conditions, resulting in higher mortality rates (Arnett et al. 2008, Baerwald and Barclay 2011, Smith and McWilliams 2016). Indeed, mortality rates among migratory bat species are higher in autumn compared with all other seasons (Arnett et al. 2008, Cryan and Barclay 2009). Lower mortality rates at wind turbines during spring and summer, compared with autumn, suggest that there exist important differences in migration behavior between seasons (Arnett et al. 2008, Grodsky et al. 2012). In eastern North America, patterns of migration in bats may be somewhat comparable to terrestrial bird migration, whereby different migratory pathways between seasons has been

observed (La Sorte et al. 2014). Furthermore, these differences between seasons are influenced by differences in seasonal atmospheric conditions.

Numerous studies have documented a positive relationship between ambient temperatures and activity of migratory tree bats during the spring and autumn, with activity generally increasing above 10 ℃ (Fiedler 2004, Kerns and Horn 2005, Baerwald and Barclay 2011, Weller and Baldwin 2012, Bender and Hartman 2015, Smith and McWilliams 2016, Dechmann et al. 2017). However, research on the effect of barometric pressure on migratory bat activity has been less conclusive. Cryan and Brown (2007), Baerwald and Barclay (2011), and Dechmann et al. (2017) all observed lower and dropping barometric pressures were correlated with increased activity, whereas others have found the opposite (Bender and Hartman 2015, Smith and McWilliams 2016). Indeed, barometric pressure may affect migratory bat activity positively and negatively: higher pressures are associated with easier flight conditions while dropping pressure may indicate a passing storm front (Richardson 1978, Smith and McWilliams 2016). Precipitation negatively affects migratory bat activity, likely due to a combination of attenuation affecting echolocation, exposure on an individual level, associated atmospheric conditions, and influence on insect prey (Griffin 1971, Arnett et al. 2007, Lacki et al. 2007). However, the effects of precipitation on bat activity may be negligible when compared to other atmospheric conditions. For example, Smith and McWilliams (2016) found that autumn migratory activity of bats in Rhode Island was less influenced by precipitation than by temperature, wind direction, and changes in pressure.

Landscape feature relief and elevation likely affects migratory bats differently between seasons and among species, and may depend on "pre-determined" migratory pathways (Reynolds 2006, Baerwald and Barclay 2009). Additionally, geographic conditions, especially elevation,

greatly influences atmospheric conditions in the Appalachians (Lindberg et al. 1988). Average

temperatures are lower whereas precipitation amount and duration are greater at higher

elevations (Lindberg et al. 1988). Furthermore, more precipitation occurs on windward slopes in

the Appalachians, and because many weather fronts travel from west to east, the Allegheny

physiographic sub-province is generally more mesic than the Ridge and Valley (Ray 1986, Soulé

1998). Among these atmospheric and geographic conditions, it is clear that ambient temperatures

affect migratory bat activity, and temperature likely interacts with other conditions such as wind

speed, wind direction, and elevation. Notably, Wolbert et al. (2014) found a significant

interaction between the effects of relative elevation and ambient temperatures on bat activity,

such that ambient temperatures had greater effects on bat activity at higher elevations.

Wind speeds are generally greater at higher elevations in the Appalachians (Lindberg et

al. 1988). However, bat mortality at wind turbines has been associated with lower wind speeds

(Fiedler 2004, Kerns and Horn 2005, Arnett et al. 2008, Baerwald and Barclay 2011). The cut-in

wind speed, whereby turbines begin to produce energy, is typically between 11 and 14.5 kph,

whereas the rated wind speed (where maximum electricity is generated) is around 40 to 56 kph.

Most bat mortality occurs around and below cut-in wind speed, when energy production is less

than optimal (Fiedler 2004, Arnett et al. 2011, Martin et al. 2017). Furthermore, greater bat

activity is associated with lower wind speeds regardless of geographic location or position

(Cryan and Brown 2007, Smith and McWilliams 2016, Dechmann et al. 2017). Additionally,

wind direction may also influence migratory bat activity, in both the fall and spring migration

periods, with tailwinds associated with increased bat activity (Smith and McWilliams 2016,

Dechmann et al. 2017). Wind direction and wind speed likely have interactive effects on

migratory bat activity (Smith and McWilliams 2016, Dechmann et al. 2017).

Recent studies suggest that simply raising turbine cut-in speed is an effective strategy to reduce a high proportion of bat mortality at wind facilities, while still maintaining economic viability (Baerwald et al. 2009, Arnett et al. 2011, Weller and Baldwin 2012, Arnett et al. 2013, Martin et al. 2017). Greater, site-specific understanding of the effect of wind speed and wind direction on migratory behavior could contribute to management practices that greatly reduce future wind energy-associated bat mortality. Identification of important migratory pathways, and geographic features associated with them could significantly reduce bat mortality associated with wind turbines through development of better, site and geography-specific curtailment strategies.

My objectives were to determine major activity patterns and define drivers thereof for migratory bat species during the autumn and spring migration periods along ridgelines and sideslopes in the central Appalachians, an area where wind energy development is increasing. I expected activity patterns to vary among migratory species both temporally and spatially. During the fall migratory period, I anticipated greater migratory bat activity at higher elevations, but greater activity at lower elevations during the spring migratory period. Furthermore, I expected that ambient conditions influence migratory bat activity during the fall and spring migratory periods in the central Appalachians. Regardless of season, I expected decreased levels of activity during periods of high wind speed, low temperatures, and during bouts of precipitation.

### Methods

*Study Area*

I conducted my study on five mountain massifs (ridges) and adjacent sideslopes in the Ridge and Valley and Blue Ridge sub-provinces of the central Appalachian Mountains in Virginia (Figure 1-1). I chose these five ridges because the maximum elevations were over

1000m, were areas denoted with high wind potential and were topographically similar to many wind farms in the mountains of the eastern United States (Virginia Center for Wind Energy). These areas included: Sugar Run Mountain (Giles County, elevation 1,238 m), Salt Pond Mountain (Giles County, elevation 1,329 m), Back Creek Mountain (Bath County, elevation 1,102 m), Big Flat Mountain (Rockingham County, elevation 1,033 m), and Hazeltop Mountain (Madison County, elevation 1,162 m). Study sites were located within Jefferson and George Washington National Forest lands or Shenandoah National Park. The forests types throughout are generally xeric-to moderately mesic oak associations on ridges with mixed mesophytic forest along drainages or sheltered north-facing slopes (Braun 1950). Multiple species of oak occur, with white oak (*Quercus alba*) and chestnut oak (*Quercus pinus*) being dominant. In lower elevations and along riparian corridors, mesic species such as eastern white pine (*Pinus strobus*), tulip poplar (*Liriodendron tulipifera*), and eastern hemlock (*Tsuga canadensis*) are common (Kniowski 2016).

*Data Collection*

I collected acoustic data using Song Meter ZC detectors with SMM-U1 microphones, Song Meter SM2 detectors with SMX-U1 microphones, and Song Meter SM4 detectors with SMM-U1 microphones (Wildlife Acoustics, Maynard, MA) from early September to mid-November in 2015 and 2016, when migratory tree bats depart summer ranges and fly south, and in early March to late April in 2016 and 2017, when bats migrate northwards and disperse across the landscape to summer ranges (Cryan 2003, Baerwald and Barclay 2011).

I deployed detectors longitudinally along ridgelines, with three detectors placed at high elevations (higher than 1000m where possible), one detector at mid-elevation (roughly halfway between the ridgetop elevation and the associated valley floor elevation, 500-750m), and one

detector at low elevation (generally less than 300 meters elevation and proximal to a valley, Figure 2-26). I used digital elevation models in ArcMap 10.3.1® (ESRI, Redlands, CA) software to derive elevation, and choose potential general detector locations at each elevation category. I programmed detectors to record nightly from 1900 to 0700 hours, and precise detector locations were chosen based on accessibility, likelihood of migratory bat presence, and site characteristics known to produce high-quality call recordings (i.e., low clutter such as a forest canopy gap/riparian corridor).

I collected hourly weather data from the airport nearest to each detector site (https://www.wunderground.com/ 2017). I created a wind profit variable by combining average wind speeds and average hourly wind directions, and used it to test if bats use tailwinds for advantageous flight during migratory seasons (Smith and McWilliams 2016). Because bats to use the linear arrangement of ridgelines to migrate north or south depending on season,I assumed that winds running parallel to ridgelines would have either a positive or negative effect on bat activity. In autumn, when average hourly winds are predominantly from the southwest, I assigned wind profit a negative value, whereas wind predominantly from the northeast incurred a positive wind value. I assigned the of inverse autumn wind profit to the spring season to account for opposite migration patterns of bats.

I identified acoustic call data to species using Kaleidoscope version 4.3.1 (Wildlife Acoustics, Maynard, Massachusetts), classifier 4.2.0 at the neutral setting, with default signal parameters (8-120 KHz frequency range, 500 maximum inter-syllable gap, two minimum number of pulses, enhanced with advanced signal processing, (USFWS: Indiana Bat Summer Survey Guidance - Automated Acoustic Bat ID Software Programs, Wildlife Acoustics - Overview of Kaleidoscope Pro 3 Analysis Software). I limited subsequent analyses to include

only call data with a minimum of three call pulses, to reduce automated species identification

errors. I manually reviewed recorded files using program AnalookW version 4.1t (Titley

Electronics, Columbia, MO) to validate automated species identification and check for

systematic and systemic errors (Lemen et al. 2015).

*Statistical Analyses*

I created a set of *a priori* candidate generalized additive mixed models (GAMMs)

representing specific hypotheses about the relationship between atmospheric and habitat

variables and hourly bat activity. I used the same variables and models for analyses of both fall

and spring data. Candidate models included additive and interactive combinations of date, hour,

site, landscape characteristics, and ambient conditions (**Error! Reference source not found.**

Table 2-26). I assessed multicollinearity among predictors using package 'corrplot' (Wei and

Simko 2016) in program R version 3.2.3 (R Core Team 2013) to ensure highly correlated

variables were not included within the same model. I tested for serial correlation in hourly bat

activity, for each species, using R package 'stats'. I fit all generalized additive mixed models

using the GAMM function from R package 'mgcv', with an autoregressive random effects

structure to account for the serial correlation of bat echolocation passes between hours at any

given site (hour nested within each unique site-date), and with a negative binomial link function

to account for overdispersion in bat pass counts (Wood 2017). I used generalized additive mixed

models because migratory bat activity may display nonlinear responses to independent variables,

and these models allow for curvilinear responses. I used an information theoretic approach to

select the best supported model, ranking models using Akaike's Information Criterion corrected

for small sample size (AIC$_c$ from package MuMIn, Bartoń 2015; Burnham and Anderson 2002).

I centered and scaled all continuous predictors to aid model fitting and to facilitate assessment of

main effects of interactions (Schielzeth 2010). I modeled activity of each species individually, and for the combined activity of all three species to assess potential differences among species as well as drivers of general bat activity in autumn and spring, regardless of year (Arnett et al. 2016).

*Results*

I sampled a total 183 site-nights during autumn 2015 and 2016, and a total 109 site-nights during spring 2016 and 2017. Due to detector failure, and inaccessibility due to weather, some detector recordings at specific sites sometimes were not continuous over the two years. Kaleidoscope identified 3,322 and 5,118 LANO acoustic passes, 2,657 and 2,512 LABO acoustic passes, and 2,051 and 892 LACI acoustic passes in data recorded during autumn 2015 and 2016, respectively. Kaleidoscope identified 3,178 and 10,851 LANO acoustic passes, 1,409 and 1,413 LABO acoustic passes, and 1,913 and 5,243 LACI acoustic passes in data recorded during spring 2016 and 2017, respectively. Although not a component of this analysis, in the autumn of 2016 and 2017, I recorded XXX and XXX of 'other' bat species, (THEN JUST LIST the species but not their species totals.. And then do this for spring

*Autumn activity patterns*

The best supported model describing total migrant hourly activity contained mean hourly temperature, date, hour of sampling, change in temperature from 4 hours prior, mean hourly barometric pressure, mean hourly wind speed, change in barometric pressure from 6 hours prior, and mean hourly wind profit (in order of decreasing effect sizes; Table 2-27). The best supported model also contained hourly precipitation (presence or absence per hour) and relative elevation (categorical variables; Table 2-27). All variables except hourly wind profit had non-zero effects. No other models had empirical support ($\Delta AIC_c < 2$). Smoothers were supported for temperature,

date, and hour (Table 2-27). All variables except mean hourly wind profit displayed non-zero effects. Activity decreased over the season with a pulse of activity in October (Figure 2-27). Activity was positively related to mean hourly temperature and negatively related to hour of sampling (Figure 2-28 and 2-Figure 2-*29*). Among the remaining continuous predictors, barometric pressure, wind speed, and change in temperature from 4 hours prior had the largest effect sizes (Table 2-27). Migrants were more active at higher barometric pressures, lower wind speeds, and when temperatures decreased more from 4 hours prior (Figure 2-30 and 2-Figure 2-*31*). Although contained in the best supported model, mean hourly wind speed, mean hourly wind profit, mean hourly barometric pressure, relative elevation, change in temperature from 4 hours prior, and change in barometric pressure from 6 hours prior had minimal effect sizes.

The best supported model describing autumn LANO hourly activity contained Julian date, mean hourly temperature, hour of sampling, change in temperature from 4 hours prior, mean hourly barometric pressure, change in barometric pressure from 6 hours prior, and mean hourly wind speed (In order of decreasing effect sizes; Table 2-28). The model also included relative elevation (categorical). No other models were competing. Smoothers were supported for temperature, date, and hour (Table 2-28). All variables except relative low elevations displayed non-zero effects. Activity levels were variable over the season with a pulse of activity in October, and were positively related to mean hourly temperature, peaking around 20 degrees (Celsius), and negatively related to hour of sampling (Figure 2-32Figure 2-33, andFigure 2-*34*, respectively). Among other continuous variables, change in temperature from 4 hours prior had the largest effect size, and activity was greater when the temperature decreased more (Figure 2-35). Activity was greatest at low elevations and lesser at higher elevations, but confidence

intervals overlapped to a large extent. Increased activity was related marginally to barometric pressure and change in pressure from 6 hours prior, but negatively related to wind speed.

The best supported model describing LABO hourly activity including hour of sampling, mean hourly wind speed, change in barometric pressure from 6 hours prior, and mean hourly wind profit (In order of decreasing effect sizes; Table 2-29). The model also included hourly binary precipitation (categorical). No other models were competing ($\Delta AIC_c < 2$). The smoother on hour was supported, and LABO activity was higher in the first few and last few hours of the night (Figure 2-36). All variables except mean hourly wind profit displayed non-zero effects. Among remaining continuous predictors, wind speed had the largest effect size (Table 2-29). Activity of LABO was related negatively with wind speed, and activity was negatively related to precipitation (Figure 2-37). Although also contained in the best supported model, wind profit and change in barometric pressure from 6 hours prior had minimal effect sizes.

I was unable to model autumn LACI activity patterns due to limited nightly echolocation passes recorded. Kaleidoscope identified 2,943 LACI acoustic passes in data recorded over both autumn sampling periods (2015 and 2016), but only 892 LACI acoustic passes (~5 passes per night/~0.4 passes per hour) were recorded during the autumn sampling period in 2016.

*Spring Activity Patterns*

The best supported model describing migrants' hourly activity contained Julian date, hour, mean hourly temperature, mean hourly wind speed, change in barometric pressure from 6 hours prior, and mean hourly wind profit (in order of decreasing effect sizes; Table 2-30). The model also included hourly binary precipitation (categorical). No other models were competing. Smoothers were supported for both hour and date (Table 2-30). All variables except mean hourly wind profit displayed non-zero effects. Activity generally increased over the season, with a peak

in mid-April, and activity was higher in the first few hours of the night (Figure 2-38 and 2-Figure 2-*39*). Among other continuous predictors, temperature had the largest effect size, and activity was related positively with temperature (Figure 2-40). Although contained in the best supported model, mean hourly wind speed had only a marginally negative effect on activity, as did change in pressure from 6 hours prior. Activity also was related negatively to hourly binary precipitation.

The best supported model describing LANO hourly activity contained Julian date, hour, mean hourly temperature, mean hourly wind speed, change in barometric pressure from 6 hours prior, and mean hourly wind profit (in order of decreasing effect sizes; Table 2-31). The model also included hourly binary precipitation (categorical). No other models were competing. Smoothers were supported for both hour and date (Table 2-31). All variables except mean hourly wind profit displayed non-zero effects. Activity generally increased over the season, with a peak in mid-April, and activity was higher in the first few hours of the night (Figure 2-41 and 2-Figure 2-*42*). Activity was related negatively to hourly precipitation. Spring LANO activity was related positively to temperature, and temperature had a large effect size (Figure 2-43). Although contained in the best supported model, mean hourly wind speed had only a marginally negative effect on activity (Figure 2-44), as did change in pressure from 6 hours prior.

The best supported model describing LABO hourly activity contained continuous variables including Julian date, hour, mean hourly temperature, mean hourly wind speed, change in barometric pressure from 6 hours prior, and mean hourly wind profit (in order of decreasing effect sizes (Table 2-32). The model also included hourly binary precipitation (categorical). No other models were competing. Among smoothed terms, both hour and date had well supported smoothers (Table 2-32). All variables except mean hourly wind profit displayed non-zero effects.

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Activity decreased slightly over the season, and activity peaked during the 3$^{rd}$ and 8$^{th}$ hour of sampled nights (Figure 2-45 and 2-Figure 2-*46*). Among other continuous predictors, temperature and wind speed had the largest effect sizes. Activity was related positively with temperature, but negatively related with wind speed and hourly binary precipitation (Figure 2-47 and 2-Figure 2-*48*). Although also included in the best supported model, wind profit and change in barometric pressure from 6 hours prior had minimal effect sizes.

The best supported model describing LACI hourly activity contained Julian date, hour of sampling, mean hourly temperature, and an interaction between date and mean hourly temperature (in order of decreasing effect sizes; Table 2-33). The model also included hourly binary precipitation (categorical). No other models were competing. Smoothers were supported for both hour and date (Table 2-33). All variables except hourly binary precipitation had non-zero effects. Activity generally increased over the season, with a peak in mid-April, and activity was higher in the first few hours of the night (Figure 2-49 and 2-Figure 2-*50*). Activity was related negatively to hourly precipitation. Among other continuous predictors, mean hourly temperature had the largest effect size, and activity was related positively to temperature (Figure 2-51). The interaction between date and temperature had minimal effect size.

*Discussion*

Migratory bat activity was related closely to temporal (date) and weather variables, notably hourly wind speed, in both autumn and spring. However, the relationship of autumn and spring activity to other environmental conditions varied among migratory bat species. My results suggest wind speed may be the best overall predictor of migratory bat activity in the central Appalachians. Corroborating previous research from other geographic regions, my data suggest that migratory bat species are more active at lower wind speeds, as is observered case throughout

these species' ranges (Fiedler 2004, Reynolds 2006, Baerwald and Barclay 2011, Weller and Baldwin 2012).

The majority of migratory bat activity occurred at winds speeds lower than the 11 to 14.5 kph cut-in wind speed common for most industrial wind turbines (Fiedler 2004). Wind turbine blades often continue to free-spin below cut-in wind speeds and are capable of causing bat mortality at these speeds (pick a citation)., Bat mortality rates can be significantly reduced by raising cut-in speeds for blade unlocking and/or at minimum, directionally feathering blades to reduce blade speed if below production cut-in wind levels (Arnett et al. 2011, 2013). Mortality reduction rates vary amongst operational mitigation experiments, but 50% or greater reduction in bat mortality is commonly achieved (Arnett et al. 2013). Projections for the economic costs of operational mitigation and annual output lost vary greatly due to differences in exact mitigation treatment implemented (i.e. seasonal duration), associated turbine technology/limitations, and geographic locations/wind patterns (Arnett et al. 2013). However, wind speeds are not the only predictor of migratory bat activity, and my results suggest that migratory bats appear to respond to atmospheric conditions differently based on geographic region. Using a combination of conditions to inform operational mitigation at wind energy facilities may further reduce migratory bat fatality rates while optimizing energy production. Accordingly, our findings could inform energy producers and regulators about potential migratory bat mortality factors to aid in the development or modification of  industry best management practices (BMP) relative to bats (Frick et al. 2017).

Previous research has found a definitive positive relationship between migratory bat species' activity and ambient temperatures, regardless of season, and my results largely follow a similar pattern (Reynolds 2006, Bender and Hartman 2015, Smith and McWilliams 2016,

Bernard and McCracken 2017). In general, hourly temperatures and date had the large effect on overall bat activity during the autumn and spring migration periods. Moreover, hourly precipitation typically suppressed migratory bat activity during the autumn and spring (Griffin 1971, Smith and McWilliams 2016). However, some differences existed between species' and species' groups relationship to environmental conditions and intra-seasonality, supporting prior research (Baerwald and Barclay 2011).

*Autumn Activity*

Date was not related closely to autumn LABO activity in my study, but in Rhode Island, Smith and McWilliams (2016) found evidence to the contrary. However, Rhode Island is well outside of LABO wintering grounds (Cryan 2003). It is possible that autumn LABO activity in this study was not related to date because sites were within the species northernmost wintering range (Davis and Lidicker 1956, Cryan 2003) (Figure 2-52). Thus, recorded LABO activity potentially could be attributable to resident individuals throughout the autumn sampling period, rather than to migrating individuals. Furthermore, Bernard and McCraken (2017) found migratory bat species were active throughout the winter months in Tennessee, across a range of ambient temperatures; similarly, temperature did not substantially affect autumn LABO activity at my study sites. Depending on ambient conditions, LABO likely restricted activity due to metabolic/thermal tradeoffs balancing insect prey availability with energy expenditures associated with active foraging behavior (Bender and Hartman 2015, Bernard and McCracken 2017). Unsurprisingly, LABO activity was lower during hours with any precipitation, likely due to reducing foraging efficiency with decreased insect activity and increasing metabolic costs associated with flight and exposure (Griffin 1971, Voigt et al. 2011).

Although date and hourly ambient temperatures appeared to have little effect on autumn LABO activity, they remained important predictors of activity for autumn LANO and grouped migrant species. The observed peak of autumn LANO activity in mid-October may correspond to a final migratory push or "wave" as suggested by McGuire et al. (2012). Furthermore, LANO, LACI, and all migrant species activity was positively related to mean hourly temperature, likely due to insect prey availability and metabolic costs of activity and/or migration in cold temperatures (Reynolds 2006, McGuire et al. 2014, Wolbert et al. 2014).

My results generally corroborate previous research on the seasonal distribution and migratory timing of migratory bat species (Cryan 2003, Johnson et al. 2003). The majority of migratory bat activity in the central Appalachians occurs somewhat later in the year compared to more northern regions where most activity (and hence wind-related mortality) occurs in August and early September (Johnson et al. 2003, Baerwald and Barclay 2011, McGuire et al. 2012, Arnett et al. 2016). In Ontario, Canada, a final autumn LANO migration "wave" occurred in mid-September (McGuire et al. 2012), nearly four weeks earlier than the final "wave" I observed in the central Appalachians. Geographic variation in the timing of major migratory pulses also has important implications regarding future wind energy development and potential bat mortality mitigation policies in the central Appalachians. Understanding timing of major "waves" of activity at multiple regions also could provide data inputs toanagers to further adjust or modify wind energy BMPs.

Contrary to my expectations, overall autumn migratory bat activity was related negatively to relative elevation. Migratory bat species may use the linear arrangement of the Ridge and Valley and Blue Ridge sub-provinces to navigate during autumn migration in the central Appalachians (Baerwald and Barclay 2009, Furmankiewicz and Kucharska 2009), but my results

provide evidence that valleys are the preferred migratory corridors in this region, rather than ridgetops. In the central Appalachians of Virginia, valleys have a higher prevalence of cleared habitats such as pasture whereas ridgetops typically are forested (Kniowski and Ford 2017). Various bat species utilize linear landscape features such as riparian areas for foraging and movement between foraging/roosting areas (Limpens and Kapteyn 1991, Ford et al. 2005), and migratory bats in the central Appalachians may be more active in areas with these features due to proximity to roosting habitat, and/or improved migrating and foraging conditions due to lack of environmental clutter (Brigham et al. 1997, Kunz et al. 2007, Drake et al. 2012, Wolbert et al. 2014, Brooks et al. 2017).

I found little evidence that wind profit substantially affects autumn migratory species' activity patterns in the central Appalachians, contrasting with previous research in Rhode Island (Smith and McWilliams 2016). However, Smith and McWilliams' (2016) acoustic detector sites were generally far from potential roosting habitat (1-2 km), whereas my detectors generally were surrounded by mature hardwood forest suitable for day-roost use. It is possible that bat activity is more affected by wind direction in open habitats than in heavily forested habitats that alter wind dynamics (Quine and Gardiner 2007).

Although the general seasonality of bat migration are known, patterns of bat activity on an hourly basis are less understood (Kunz 1973, Baerwald and Barclay 2011). Hour (of sampling) each night generally had a negative effect on overall migratory bat activity during autumn, with most activity occurring within the first few hours of night, similar to previous findings (Kunz 1973). However, LABO displayed a unimodal response to hour of nightly sampling in autumn, suggesting these bats are likely foraging in the first hours after sunset, and the last few hours prior to sunrise (Kunz 1973, Kunz and Lumsden 2003, Kunz 2013). Eastern

red bats are known to forage early in the evening (sometimes before sunset), and may be active at slightly different times of day due to differences in prey availability, day-roost selection and proximity to foraging areas, or even interspecific temporal niche partitioning (Kunz 1973).

*Spring Activity*

Spring migratory bat activity was related to date, and ambient temperature was an important driver of activity for all migratory species and species groups in the spring season (Reynolds 2006, Bender and Hartman 2015, Smith and McWilliams 2016, Bernard and McCracken 2017). Similar to autumn migratory bat activity, spring activity is related positively with ambient temperature likely due to insect prey availability and metabolic costs of migration/flight in cold temperatures (Reynolds 2006, McGuire et al. 2014, Wolbert et al. 2014). Overall migratory bat activity increased through the spring sample season, but displayed defined peaks of activity, again suggesting that bats may migrate in 'waves' during the spring months, similar to autumn activity. These spring 'waves' also may be correlated with ambient conditions, such as temperatures. Activity of all migratory species grouped and LACI and LANO individually peaked in mid-April in the central Appalachians of Virginia. However, spring activity of LABO decreased slightly through time, in contrast to what I expected. These data may suggest that LABO wintering in the central Appalachians may migrate (likely northward) in spring, and a subsequent "wave" of LABO had yet to arrive prior to late April. Pulses or "waves" of activity in the spring season may be caused by differences in migration timing between sexes, or differences in wintering grounds between sexes (Cryan 2003, Cryan and Wolf 2003, Jonasson and Guglielmo 2016). Similar timing and patterning of activity has been observed north of my study area (Cryan 2003, Reynolds 2006, Grodsky et al. 2012).

Contrary to my expectations, elevation was not included within the best supported model describing spring activity for any migratory species or species group. Greater recorded mortality rates during fall migration at wind energy sites suggest migratory bats use higher elevations/ridgelines more during the fall and lower elevations/valleys during spring migration (Johnson et al. 2003, Reynolds 2006, Grodsky et al. 2012). My results indicate migratory bat activity is more evenly dispersed across the landscape in the spring compared with autumn (Johnson et al. 2003). Sex and reproductive condition may contribute to different migration patterns between autumn and spring as suggested by Jonasson and Guglielmo (2016). Female migratory bats leave wintering grounds earlier than males (Cryan 2003), and likely use torpor less than males during the spring due to pregnancy (Ford et al. 2002, Turbill and Geiser 2006, Dzal and Brigham 2013). Without extensive use of torpor during spring migration, female migratory bats need to forage more to cope with thermoregulatory costs incurred by low ambient temperatures (Ford et al. 2002, Cryan and Wolf 2003, Jonasson and Guglielmo 2016). Increased foraging behavior of female migratory bats during spring migration compared to autumn migration may explain why my results suggest more widespread migratory bat activity on the landscape, with relative elevation having little influence on activity.

Wind speed was not included in the best supported model describing spring LACI activity, suggesting other ambient conditions may have greater influence on their behavior, possibly due to larger bodies and more powerful flight compared to other migratory species (Barbour and Davis 1969, Salcedo et al. 1995, Riskin et al. 2010). However, LACI may be affected by wind speeds, but the relationship could be difficult to identify because data were limited. For instance, actively migrating bats may fly outside the range of detection (higher

and/or during different atmospheric conditions) or that they do not forage during migration flight.

Due to the nature of acoustic data, it is not possible to distinguish between a bat that is foraging and a bat that is migrating. I assumed that more acoustic activity inherently was related to greater numbers of migrating bats, but this actual relationship is untested. Previous research in Illinois has suggested that actively migrating bats may occasionally use visual cues as an alternative to echolocation therefore less likely to be detected during acoustic surveys (Timm 1989). Therefore, my results may be underestimating the number of bat passes at my sampled sites. However, in Europe, migratory bat species use echolocation during migration periods (Furmankiewicz and Kucharska 2009), therefore my acoustic detectors likely recorded such activity of bats that included migratory activity (Cryan et al. 2014, Smith and McWilliams 2016).

A detailed, regional understanding of the effects of atmospheric conditions, date, and landscape features on migratory bat activity will allow land managers to better assess the risk of bat mortality at future wind energy development sites, as well as offering potential pathways to maximize power output while reducing bat mortality at existing wind energy sites. Further elucidating migratory bat activity patterns, especially in autumn, could influence future wind turbine operational mitigation regimens, allowing for both maximum power generation while minimizing bat mortality (Arnett et al. 2013, Martin et al. 2017).

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*Tables*

Table 2-25: Variables used in candidate models representing hypotheses regarding migratory bat activity along five ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during autumn 2015 and 2016, and spring 2016 and 2017. Variables were used in different combinations, and highly correlated variables were not included within a single candidate model.

| Variable name | Variable Explanation |
| --- | --- |
| Date | week of year for fall; day of year for spring |
| Hour | hour of acoustic recording; 0-11 |
| Avg. Temp. | mean hourly temperature |
| Delta Temp. | change in mean hourly temperature from 4 hours prior |
| Avg. Wind | mean hourly wind speed |
| Avg. Wind Profit | mean hourly wind profit; combination of wind speed and direction |
| Avg. Pressure | mean hourly barometric pressure |
| Delta Pressure | change in mean hourly pressure from 6 hours prior |
| Relative elevation | proximal to valley floor, mid-slope, or ridgetop |

Table 2-26: Variables used in candidate models describing bat activity with justification and supporting literature for each parameter. Candidate models represented hypotheses regarding bat activity along five ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during autumn 2015 and 2016, and spring 2016 and 2017.

| Parameter | Justification | Supporting Literature |
|---|---|---|
| Date | Bat activity varies in intensity and spatially by date | (Cryan 2003, Baerwald and Barclay 2009, Hamilton 2012) |
| Hour of night | Bat activity varies throughout each night | (Kunz 1973, Kunz and Lumsden 2003, Kunz 2013) |
| Mean hourly temperature | Ambient temperatures affect bat activity | (Reynolds 2006, Weller and Baldwin 2012, Smith and McWilliams 2016) |
| Change in mean temperature from hours prior | Bats likely can sense even small temperature changes and adjust behavior accordingly | (Kunz 2013, Smith and McWilliams 2016) |
| Mean hourly wind speed | Bat activity generally decreases with high wind speeds | (Baerwald and Barclay 2011, Weller and Baldwin 2012, Smith and McWilliams 2016) |
| Mean hourly wind profit | Bats likely can sense wind direction and speed and adjust behavior accordingly | (Smith and McWilliams 2016) |
| Mean hourly barometric pressure | Bats may respond to barometric pressure due to flight conditions or associated conditions | (Baerwald and Barclay 2011, Bender and Hartman 2015, Smith and McWilliams 2016) |
| Change in mean pressure from hours prior | Bats may respond to changing pressure and associated changing conditions | (Baerwald and Barclay 2011, Smith and McWilliams 2016) |
| Relative elevation | Bat activity varies along an elevational gradient | (Wolbert et al. 2014) |

Table 2-27:  Relationship between hourly activity of migratory bats (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) and regional hourly atmospheric conditions along 5 ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during autumn 2015 and 2016.

| Variable | Estimate | Std..Error | Lower C.I. | Upper C.I. |
|----------|----------|------------|------------|------------|
| (Intercept) | -1.51 | 0.04 | -1.59 | -1.42 |
| Precipitation | -0.35 | 0.15 | -0.65 | -0.05 |
| Delta Temp. | -0.24 | 0.05 | -0.33 | -0.15 |
| Low elevation | 0.22 | 0.09 | 0.05 | 0.39 |
| Mid elevation | -0.22 | 0.09 | -0.38 | -0.05 |
| Pressure | 0.21 | 0.04 | 0.14 | 0.29 |
| Wind speed | -0.19 | 0.04 | -0.27 | -0.11 |
| Delta pressure | 0.07 | 0.04 | -0.01 | 0.14 |
| Wind profit | -0.04 | 0.04 | -0.11 | 0.03 |
| Smoothed Terms | edf | Ref.df | | |
| Temperature | 7.56 | 7.56 | | |
| Hour | 2.77 | 2.77 | | |
| Week | 6.84 | 6.84 | | |

Table 2-28: Relationship between hourly activity of silver-haired bats (*Lasionycteris noctivagans*) and regional hourly atmospheric conditions along 5 ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during autumn 2015 and 2016.

| Variable | Estimate | Std..Error | Lower C.I. | Upper C.I. |
|---|---|---|---|---|
| (Intercept) | -2.57 | 0.05 | -2.67 | -2.47 |
| Delta Temp. | -0.45 | 0.05 | -0.56 | -0.35 |
| Mid elevation | -0.20 | 0.10 | -0.40 | 0.01 |
| Pressure | 0.14 | 0.04 | 0.06 | 0.23 |
| Delta pressure | 0.12 | 0.04 | 0.03 | 0.20 |
| Wind speed | -0.11 | 0.05 | -0.21 | -0.02 |
| Low elevation | 0.03 | 0.10 | -0.17 | 0.23 |
| Smoothed Terms | edf | Ref.df | | |
| Temperature | 7.19 | 7.19 | | |
| hour | 1.56 | 1.56 | | |
| Week | 7.19 | 7.19 | | |

Table 2-29: Relationship between hourly activity of eastern red bats (*Lasiurus borealis*) and regional hourly atmospheric conditions along 5 ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during autumn 2015 and 2016.

| Variable | Estimate | Std..Error | Lower C.I. | Upper C.I. |
|---|---|---|---|---|
| (Intercept) | -2.33 | 0.04 | -2.42 | -2.25 |
| Precipitation | -0.66 | 0.19 | -1.03 | -0.29 |
| Wind speed | -0.49 | 0.04 | -0.58 | -0.41 |
| Delta pressure | -0.10 | 0.04 | -0.18 | -0.01 |
| Wind profit | 0.06 | 0.04 | -0.02 | 0.14 |
| Smoothed Terms | edf | Ref.df | | |
| Hour | 4.29 | 4.29 | | |

Table 2-30: Relationship between hourly activity of migratory bats (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) and regional hourly atmospheric conditions along 5 ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during spring 2016 and 2017.

| Variable | Estimate | Std..Error | Lower C.I. | Upper C.I. |
|---|---|---|---|---|
| (Intercept) | -0.93 | 0.05 | -1.04 | -0.83 |
| Precipitation | -1.18 | 0.23 | -1.64 | -0.72 |
| Temp. | 0.95 | 0.06 | 0.82 | 1.07 |
| Wind speed | -0.16 | 0.07 | -0.29 | -0.03 |
| Delta pressure | -0.12 | 0.06 | -0.23 | -0.01 |
| Wind profit | 0.07 | 0.07 | -0.06 | 0.20 |
| Smoothed Terms | edf | Ref.df | | |
| Hour | 4.94 | 4.94 | | |
| Day number | 8.33 | 8.33 | | |

Table 2-31: Relationship between hourly activity of silver-haired bats (*Lasionycteris noctivagans*) and regional hourly atmospheric conditions along 5 ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during spring 2016 and 2017.

| Variable | Estimate | Std..Error | Lower C.I. | Upper C.I. |
|---|---|---|---|---|
| (Intercept) | -1.77 | 0.06 | -1.89 | -1.66 |
| Precipitation | -1.97 | 0.27 | -2.49 | -1.44 |
| Temp. | 1.02 | 0.07 | 0.87 | 1.16 |
| Wind speed | -0.26 | 0.08 | -0.41 | -0.11 |
| Delta pressure | -0.13 | 0.07 | -0.26 | 0.01 |
| Wind profit | 0.05 | 0.08 | -0.10 | 0.20 |
| Smoothed Terms | edf | Ref.df | | |
| Hour | 4.05 | 4.05 | | |
| Day number | 8.31 | 8.31 | | |

Table 2-32: Relationship between hourly activity of eastern red bat (*Lasiurus borealis*) and regional hourly atmospheric conditions along 5 ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during spring 2016 and 2017.

| Variable | Estimate | Std..Error | Lower C.I. | Upper C.I. |
|---|---|---|---|---|
| (Intercept) | -2.76 | 0.06 | -2.87 | -2.64 |
| Precipitation | -0.95 | 0.26 | -1.46 | -0.45 |
| Wind speed | -0.72 | 0.07 | -0.87 | -0.58 |
| Temp. | 0.66 | 0.07 | 0.52 | 0.79 |
| Delta pressure | -0.12 | 0.07 | -0.25 | 0.01 |
| Wind profit | 0.07 | 0.07 | -0.08 | 0.21 |
| Smoothed Terms | edf | Ref.df | | |
| Hour | 6.11 | 6.11 | | |
| Day number | 1.00 | 1.00 | | |

Table 2-33: Relationship between hourly activity of hoary bats (*Lasiurus cinereus*) and regional hourly atmospheric conditions along 5 ridgelines and adjacent sideslopes in the central Appalachians, Virginia, during spring 2016 and 2017.

| Variable | Estimate | Std.Error | Lower C.I. | Upper C.I. |
|---|---|---|---|---|
| (Intercept) | -2.23 | 0.06 | -2.35 | -2.12 |
| Temp. | 0.91 | 0.06 | 0.79 | 1.03 |
| Precipitation | -0.41 | 0.23 | -0.87 | 0.05 |
| Temp.*Day number | 0.17 | 0.06 | 0.06 | 0.29 |
| Smoothed Terms | edf | Ref.df | | |
| Hour | 1.00002 | 1.00002 | | |
| Day number | 5.02825 | 5.02825 | | |
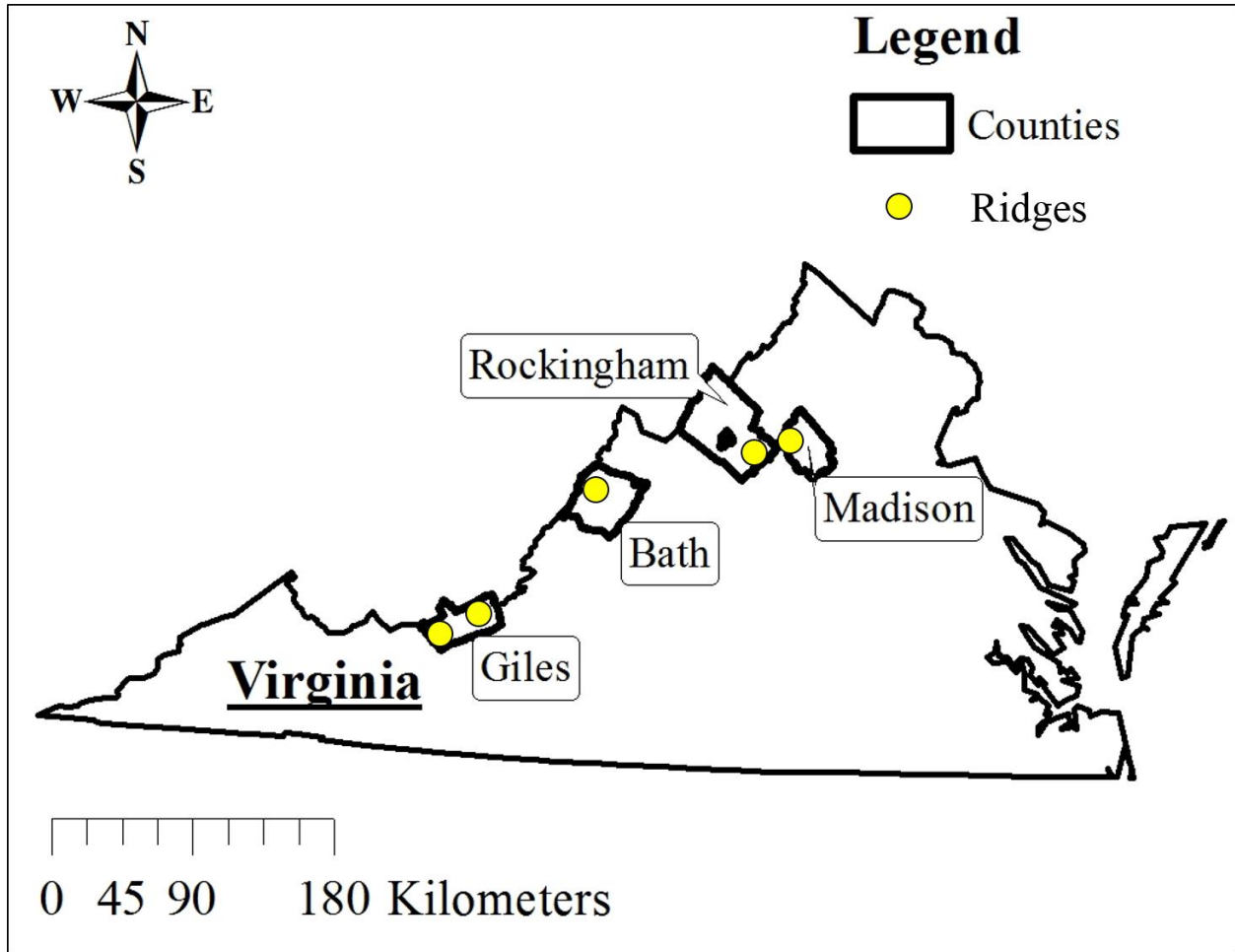
Figure 2-25: Approximate locations of five ridges sampled in central Appalachians of Virginia. The ridges sampled in Giles and Bath counties occur in the Ridge and Valley sub-physiographic province, whereas the ridges sampled in Rockingham and Madison counties occur in the Blue Ridge sub-physiographic province. Acoustic sampling occurred during autumn 2015 and 2016 and spring 2016 and 2017.
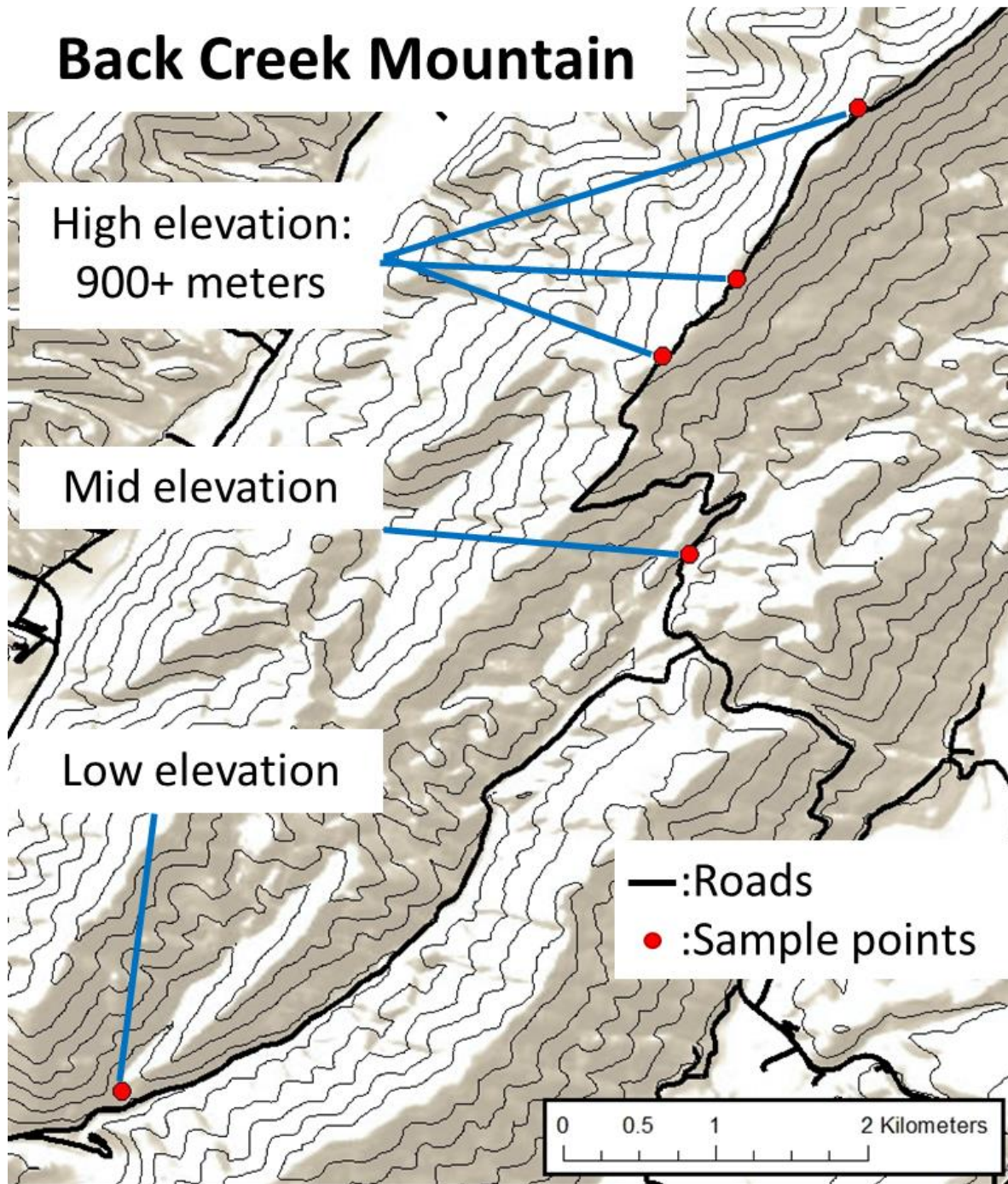
Figure 2-26: Example of acoustic sampling survey sites on ridgelines and adjacent sideslopes. Acoustic detectors were deployed in this manner along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016 and spring 2016 and 2017.
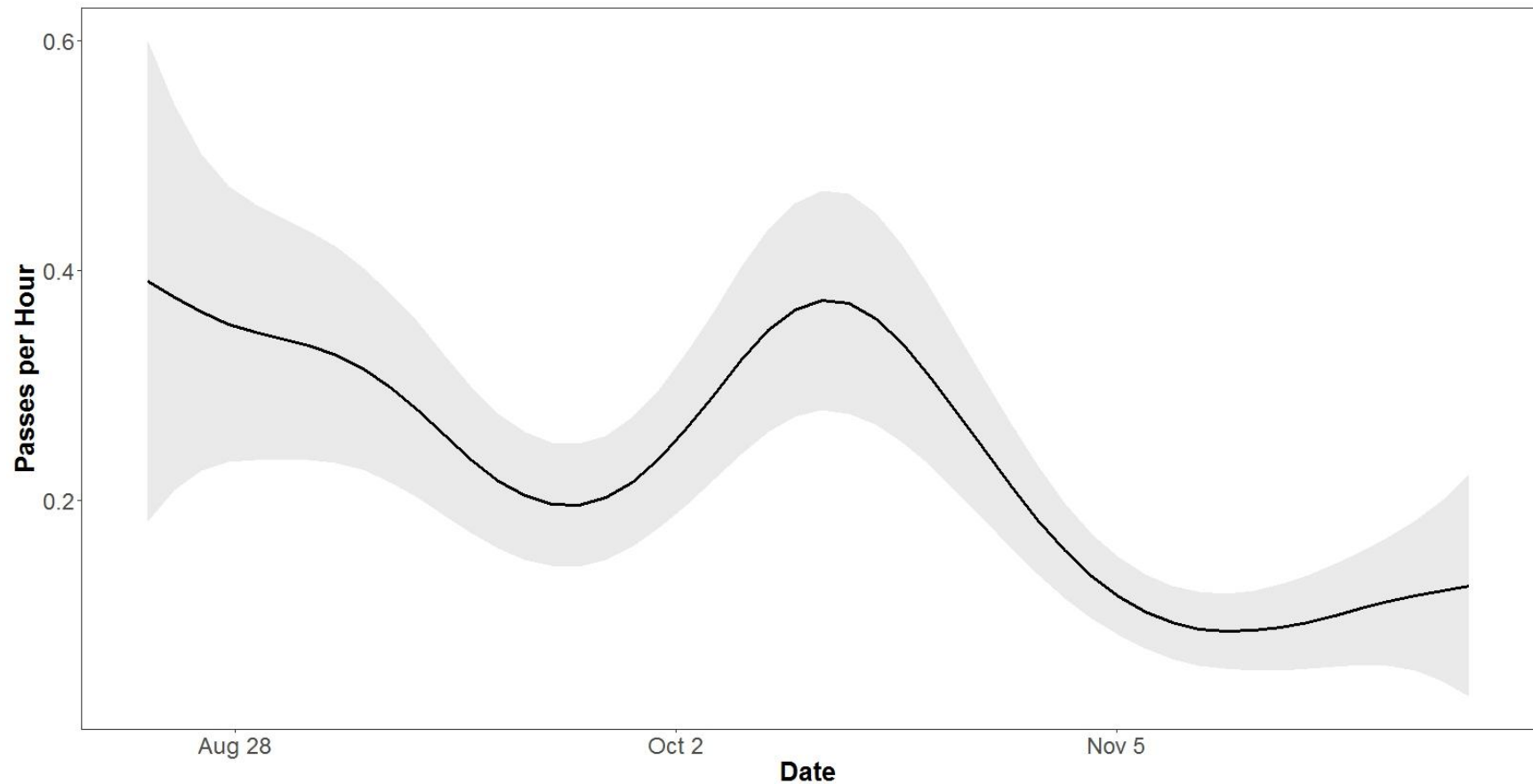
Figure 2-27: Partial effects plot of the relationship between date and migratory bat species (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
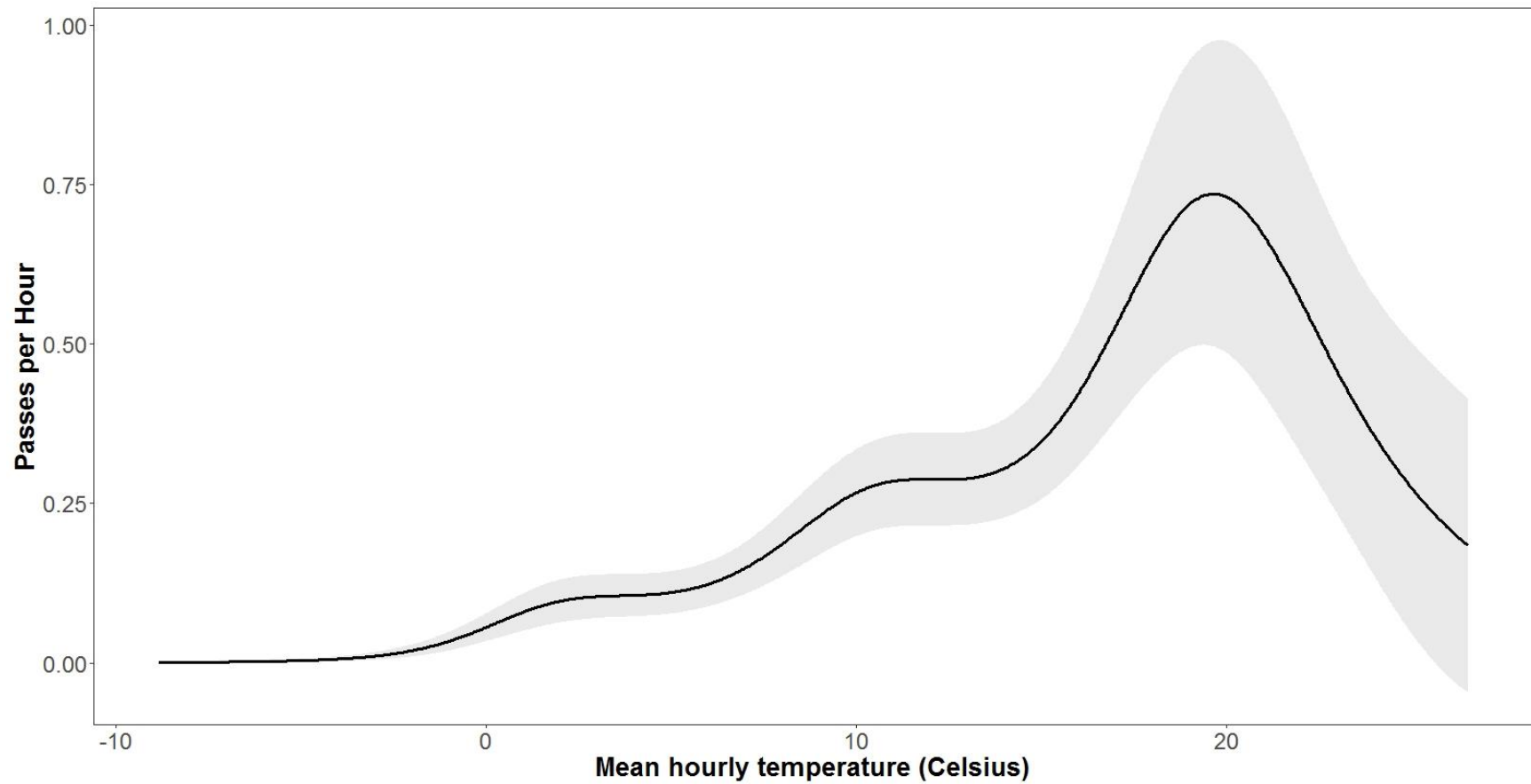
Figure 2-28: Partial effects plot of the relationship between mean hourly temperature (Celsius) and migratory bat species (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
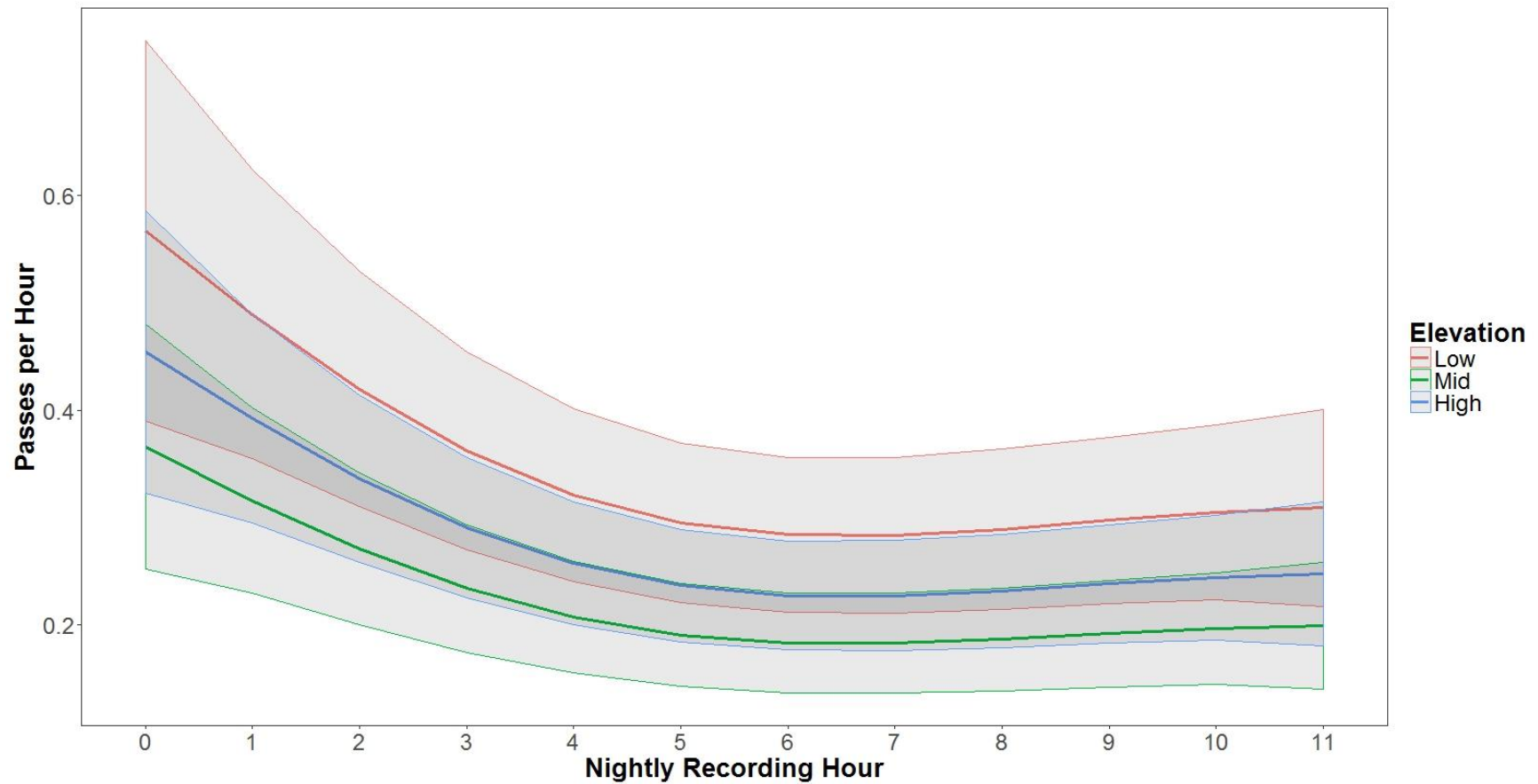
Figure 2-29: Partial effects plot of the relationship between hour of night, relative elevation, and migratory bat species (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
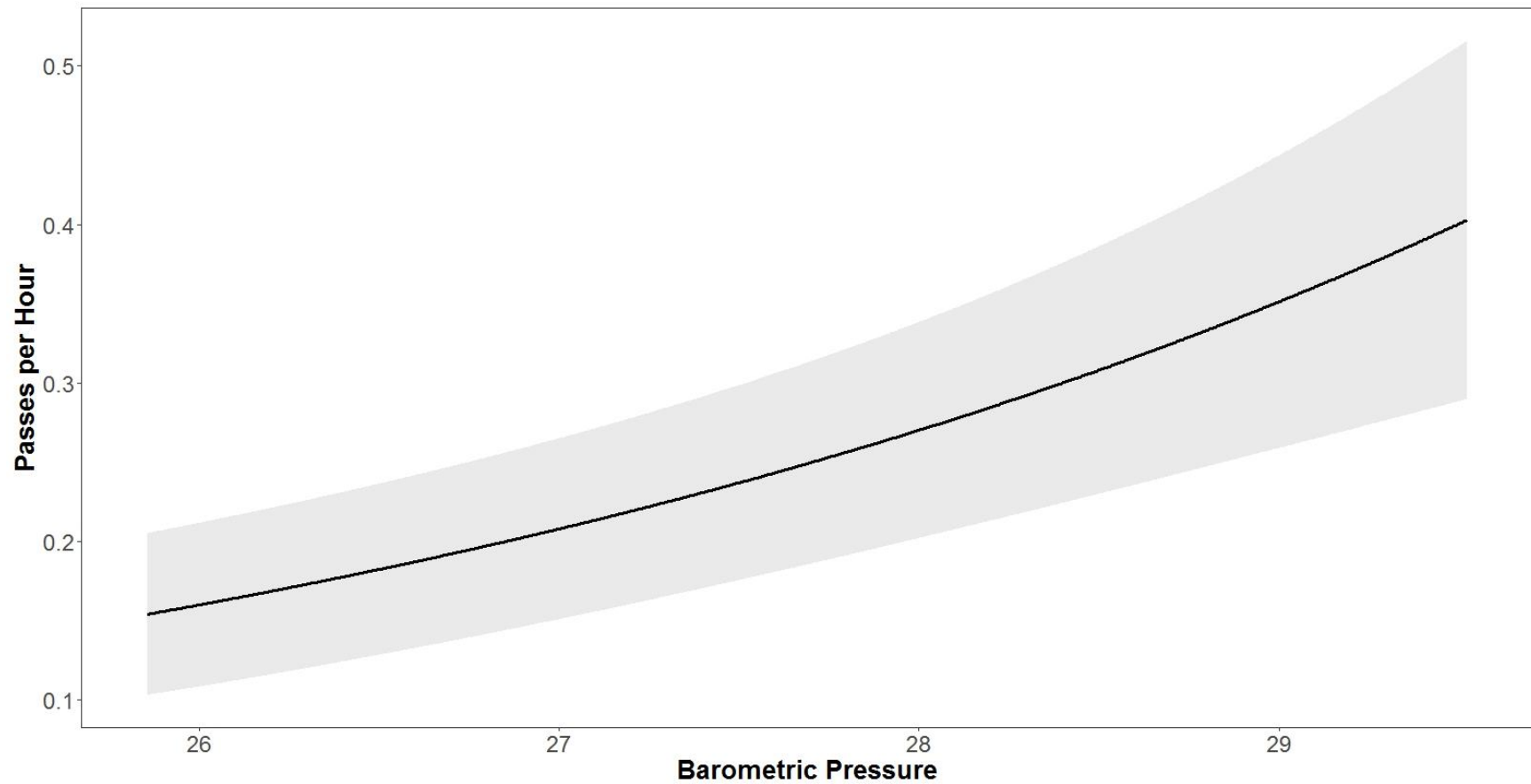
Figure 2-30: Partial effects plot of the relationship between hourly barometric pressure and migratory bat species (silver-haired bat-*Lasiurus noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
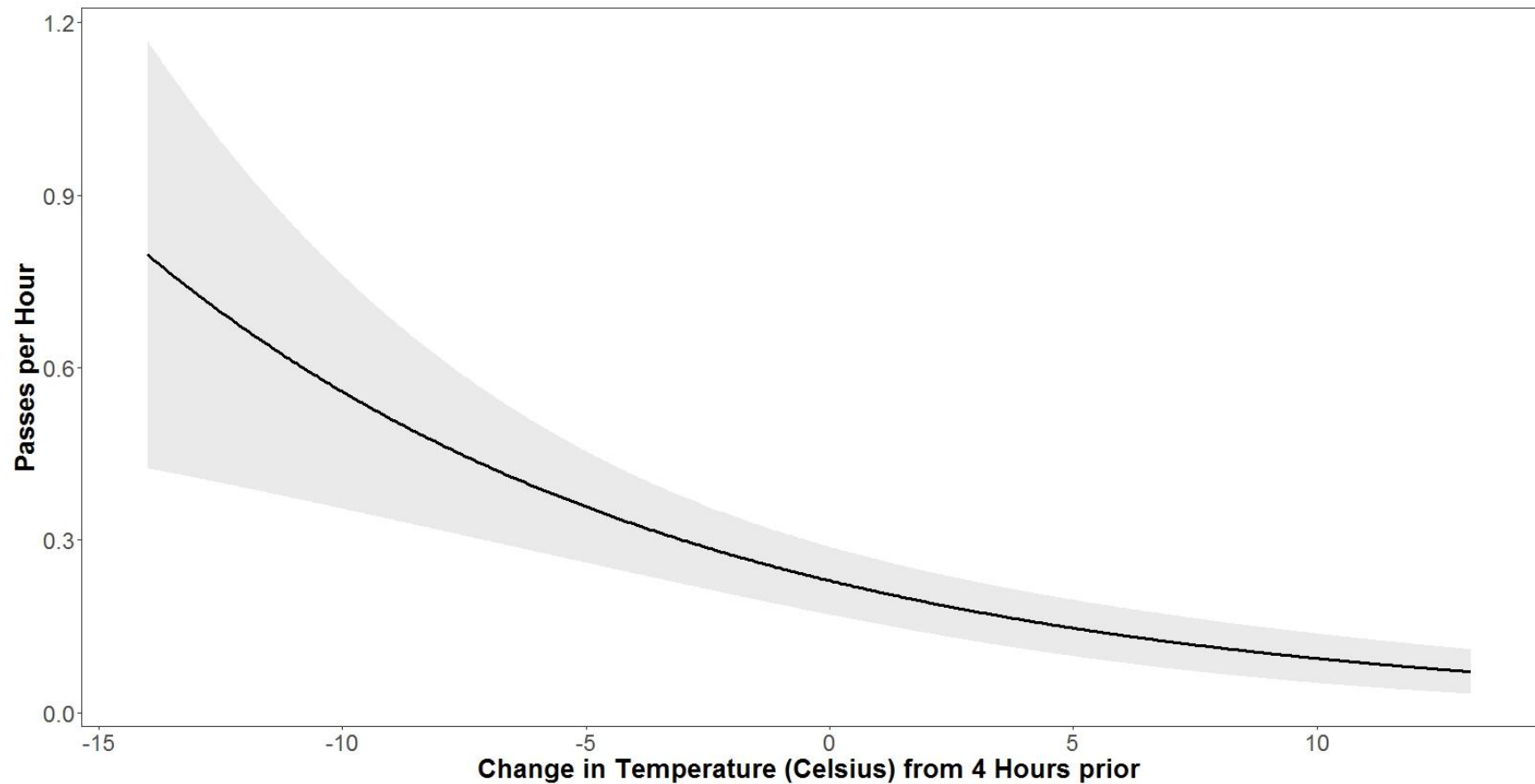
Figure 2-31: Partial effects plot of the relationship between change in ambient temperature from 4 hours prior and migratory bat species (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016. Activity was greater when the drop in temperature from 4 hours prior was greater.
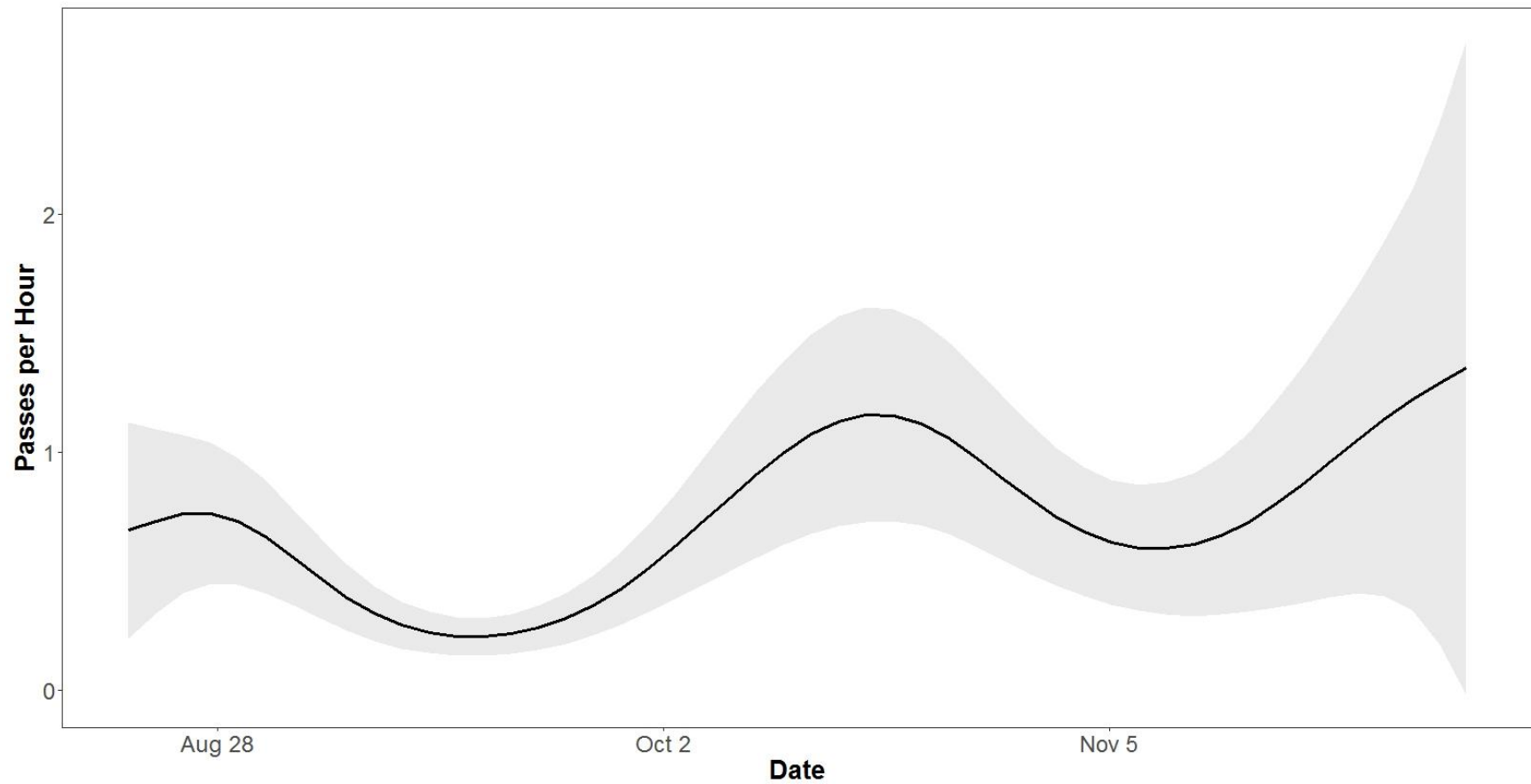
Figure 2-32: Partial effects plot of the relationship between date and silver-haired bat (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
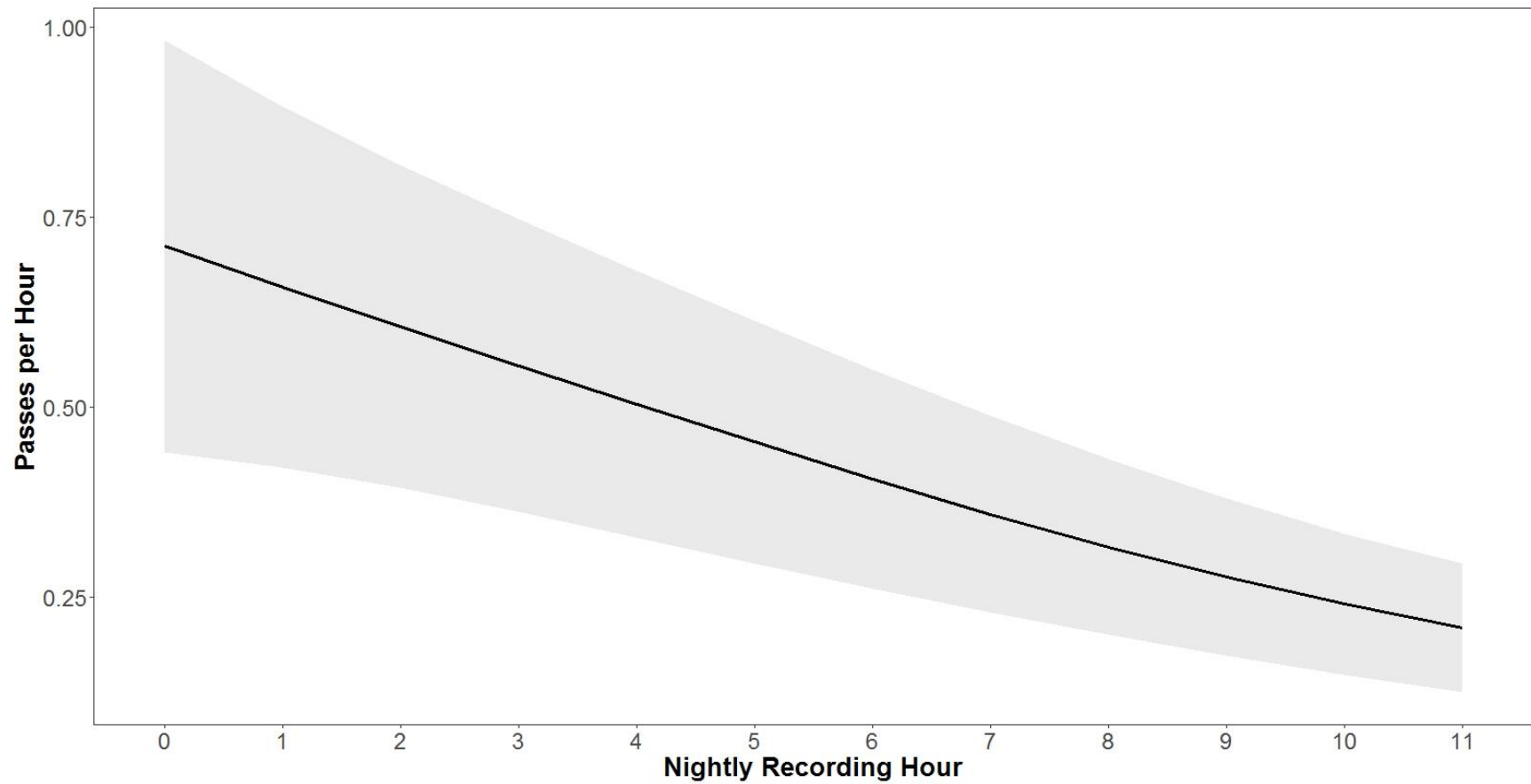
Figure 2-33: Partial effects plot of the relationship between hour of sampling each night and silver-haired bat (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
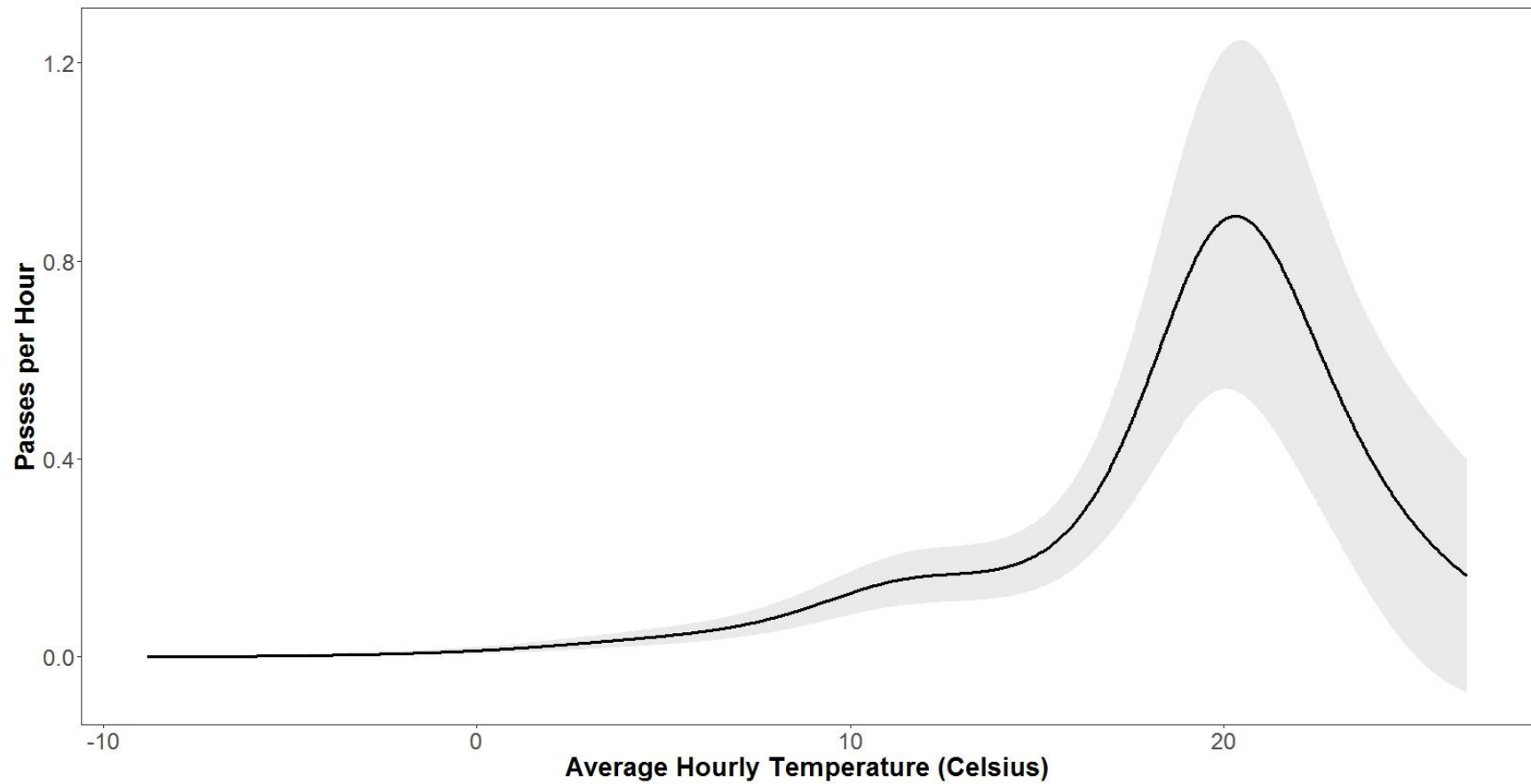
Figure 2-34: Partial effects plot of the relationship between mean hourly ambient temperature (Celsius) and silver-haired bat (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
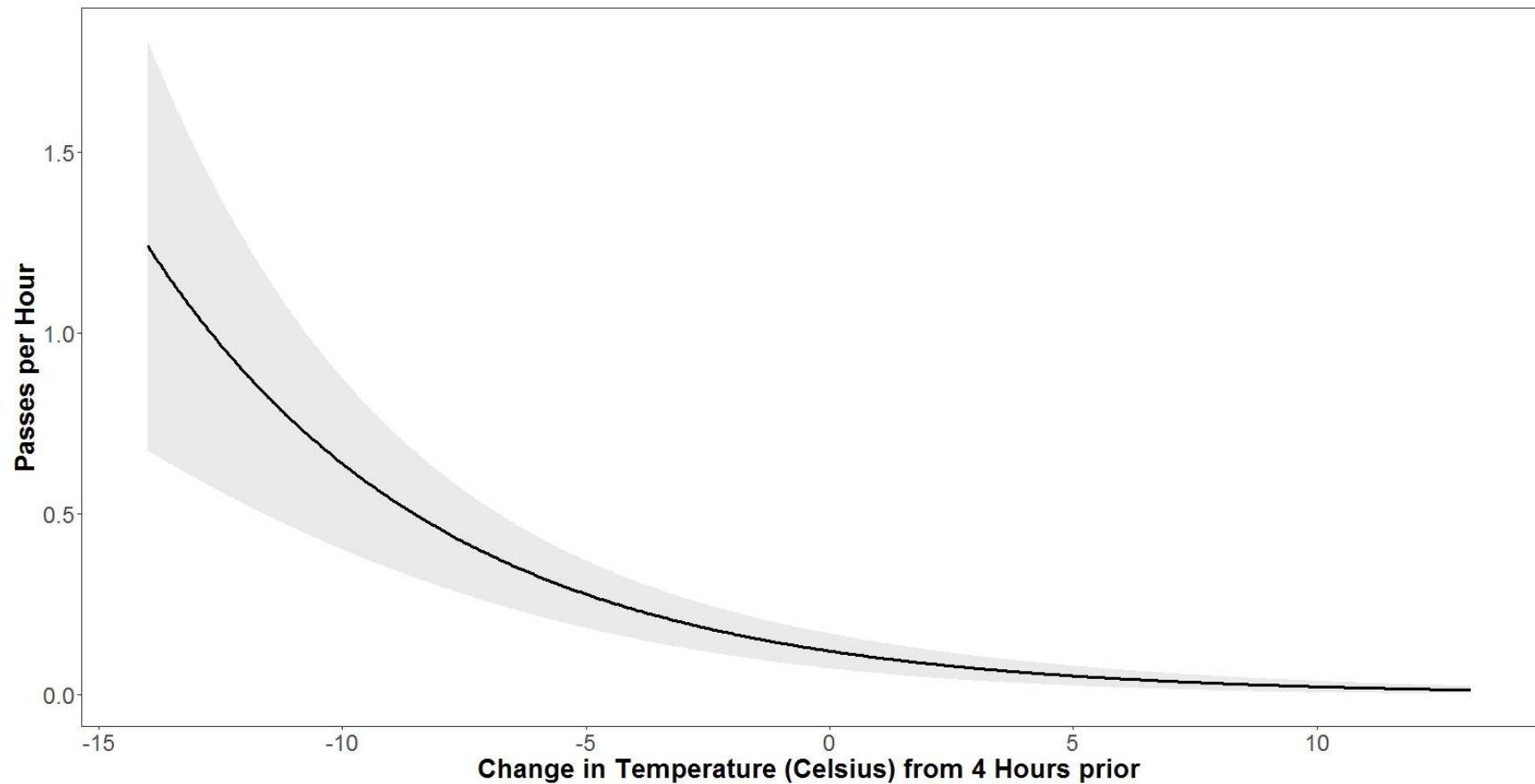
Figure 2-35: Partial effects plot of the relationship between change in ambient temperature from 4 hours prior and silver-haired bats (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016. Activity was greater when the drop in temperature from 4 hours prior was greater.
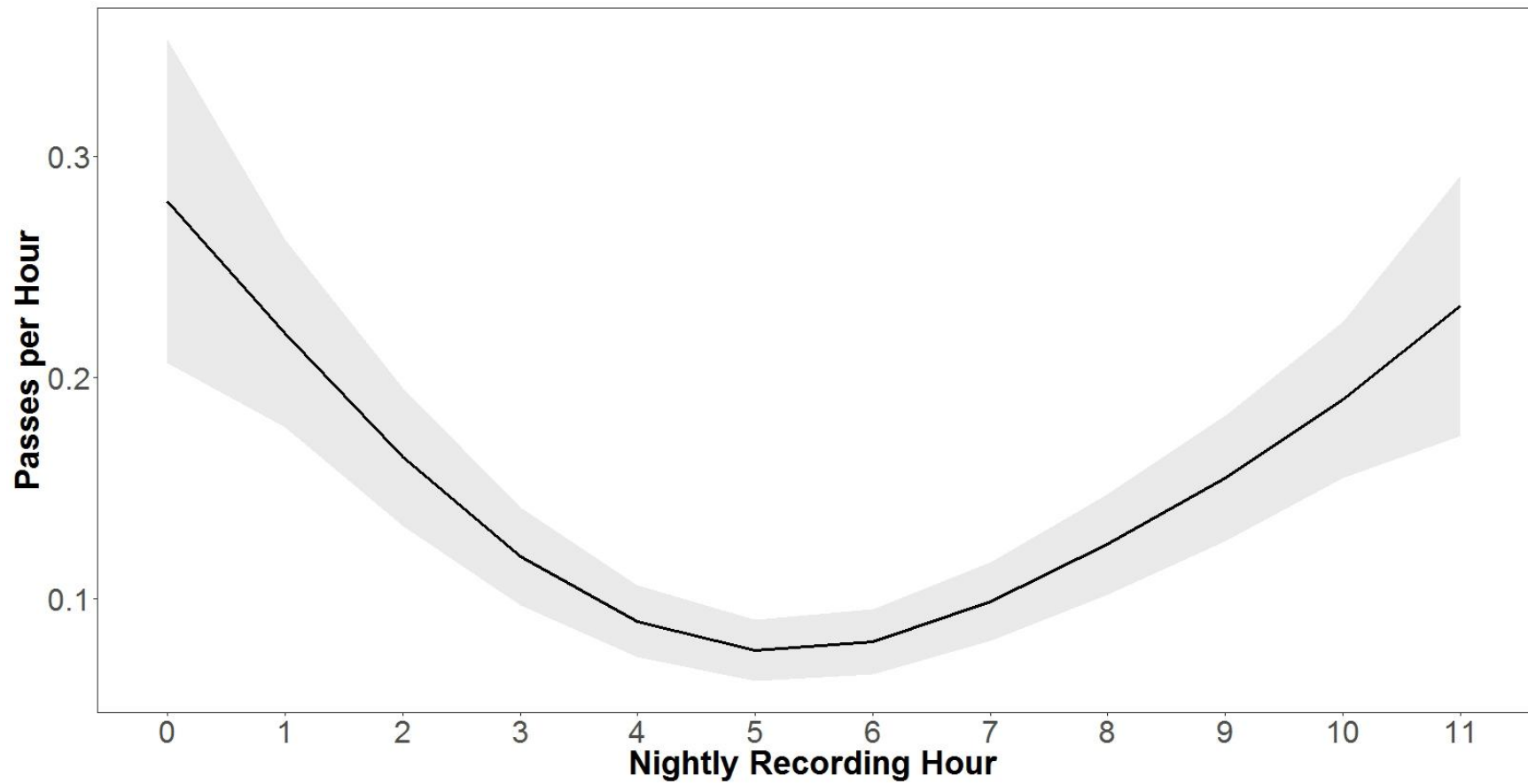
Figure 2-36: Partial effects plot of relationship between hour of sampling each night and eastern red bat (*Lasiurus borealis*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
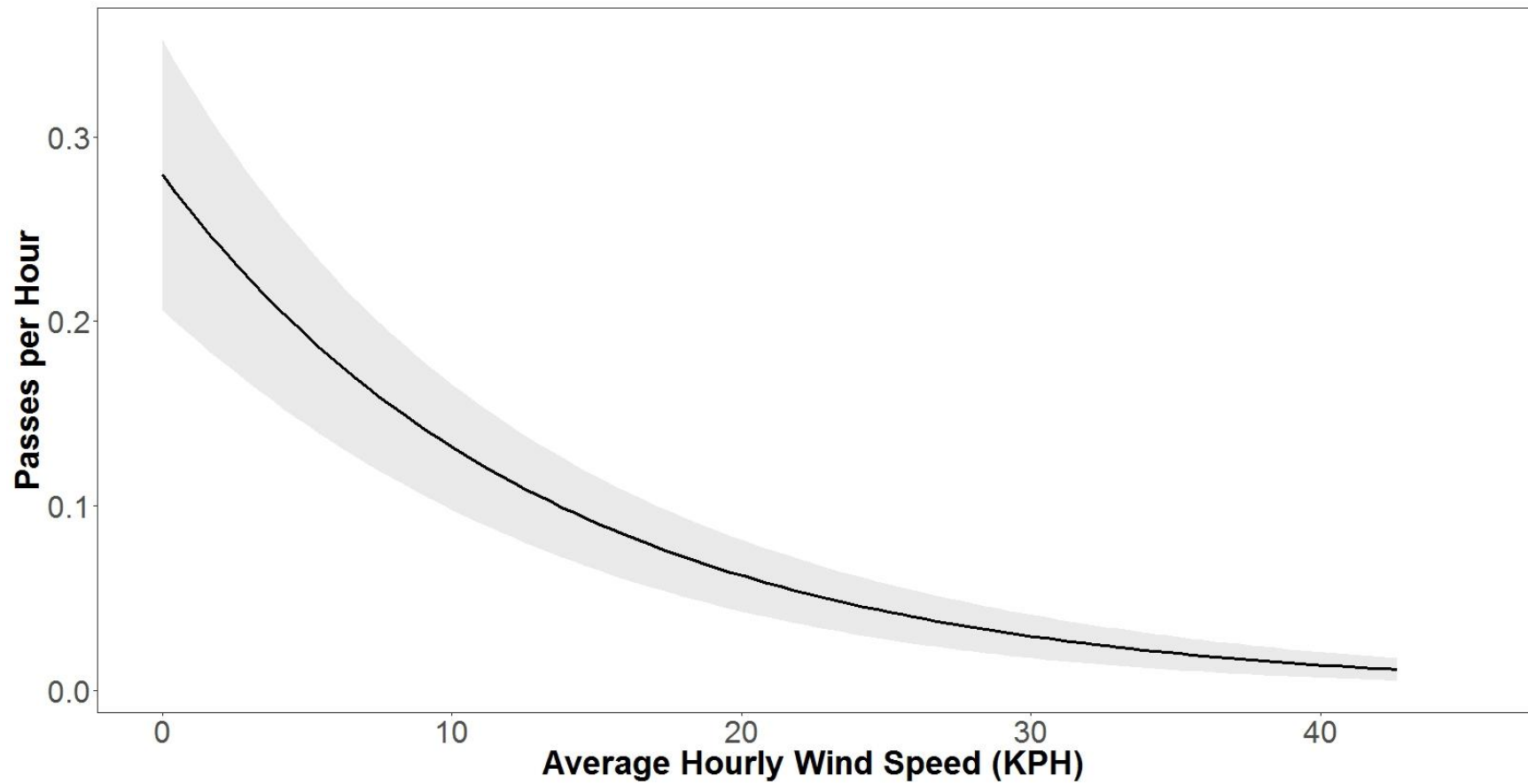
Figure 2-37: Partial effects plot of the relationship between mean hourly wind speed (KPH) and eastern red bat (*Lasiurus borealis*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during autumn 2015 and 2016.
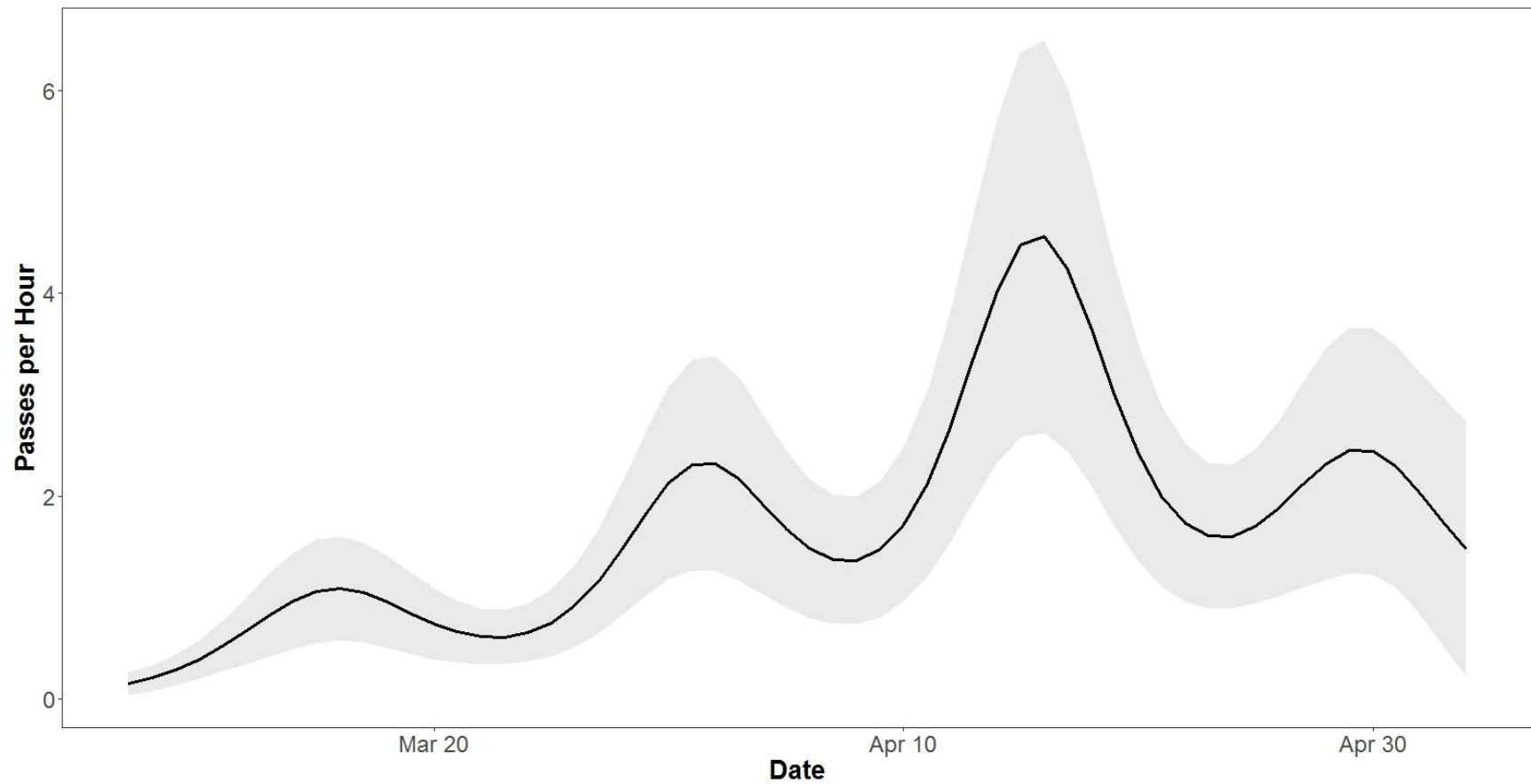
Figure 2-38: Partial effects plot of the relationship between date and eastern migratory bat species (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
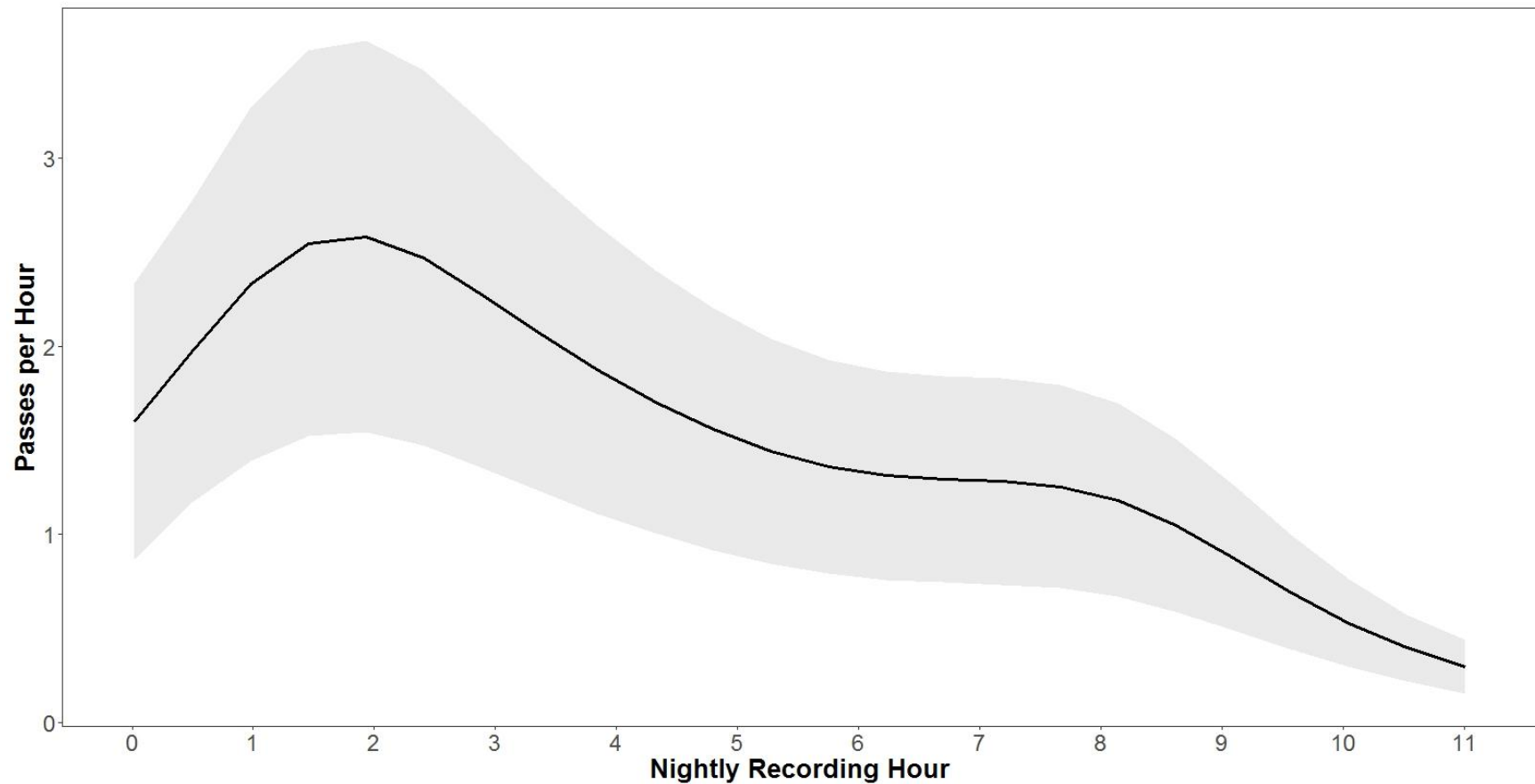
Figure 2-39: Partial effects plot of the relationship between sampling hour of night and migratory bat species (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
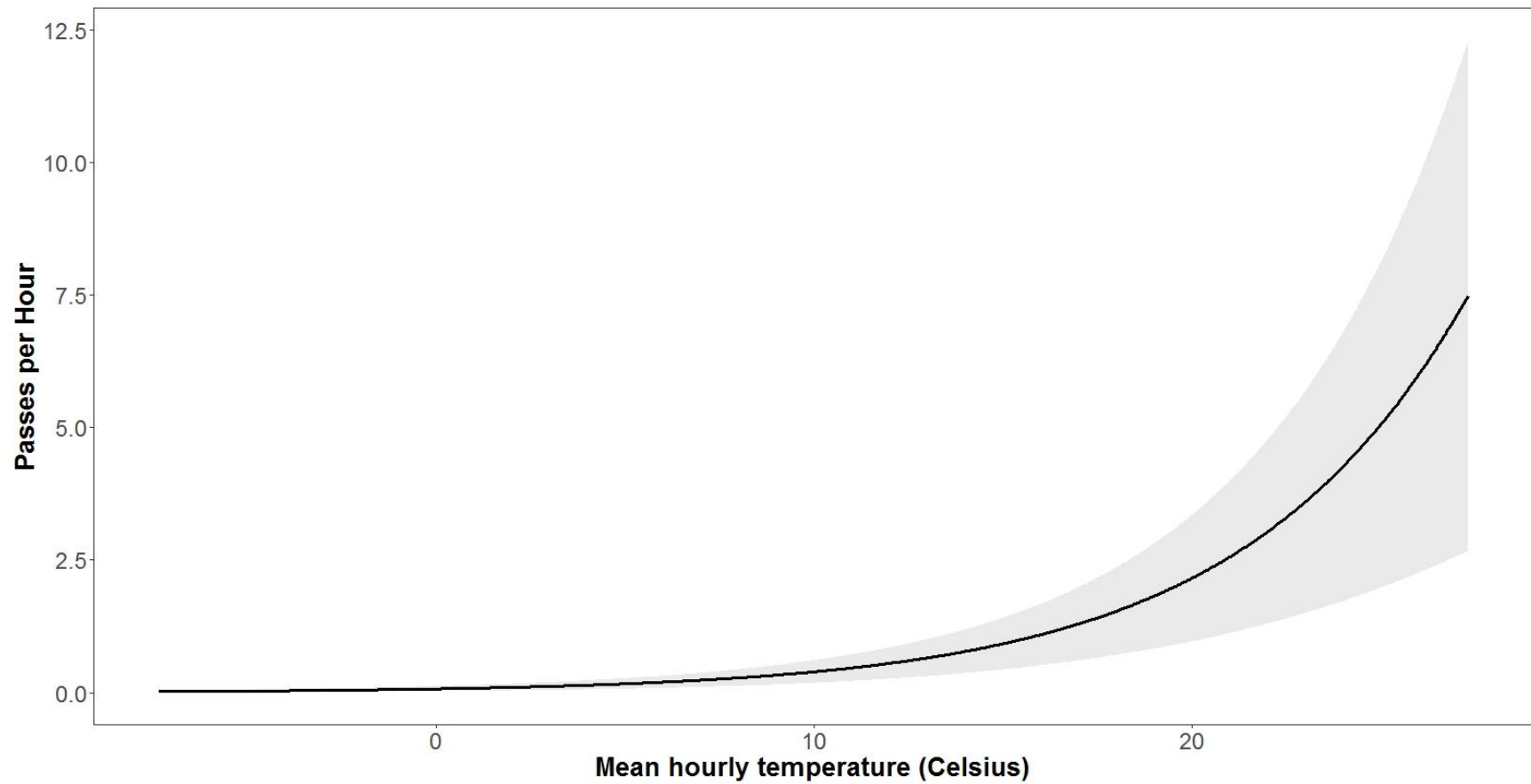
Figure 2-40: Partial effects plot of the relationship between ambient hourly temperature (Celsius) and migratory bat species (silver-haired bat-*Lasionycteris noctivagans,* eastern red bat-*Lasiurus borealis,* hoary bat-*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
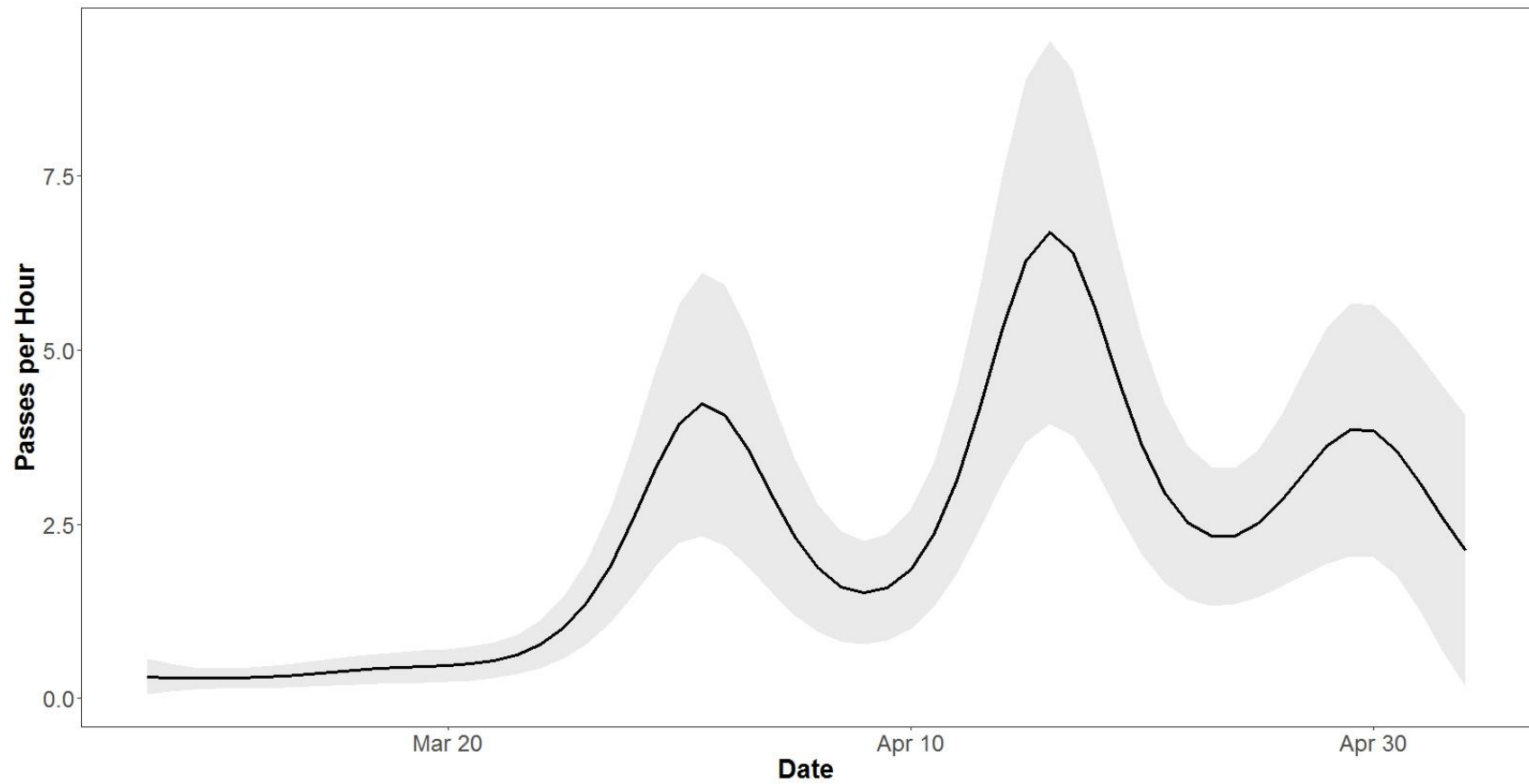
Figure 2-41: Partial effects plot of the relationship between date and silver-haired bat (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
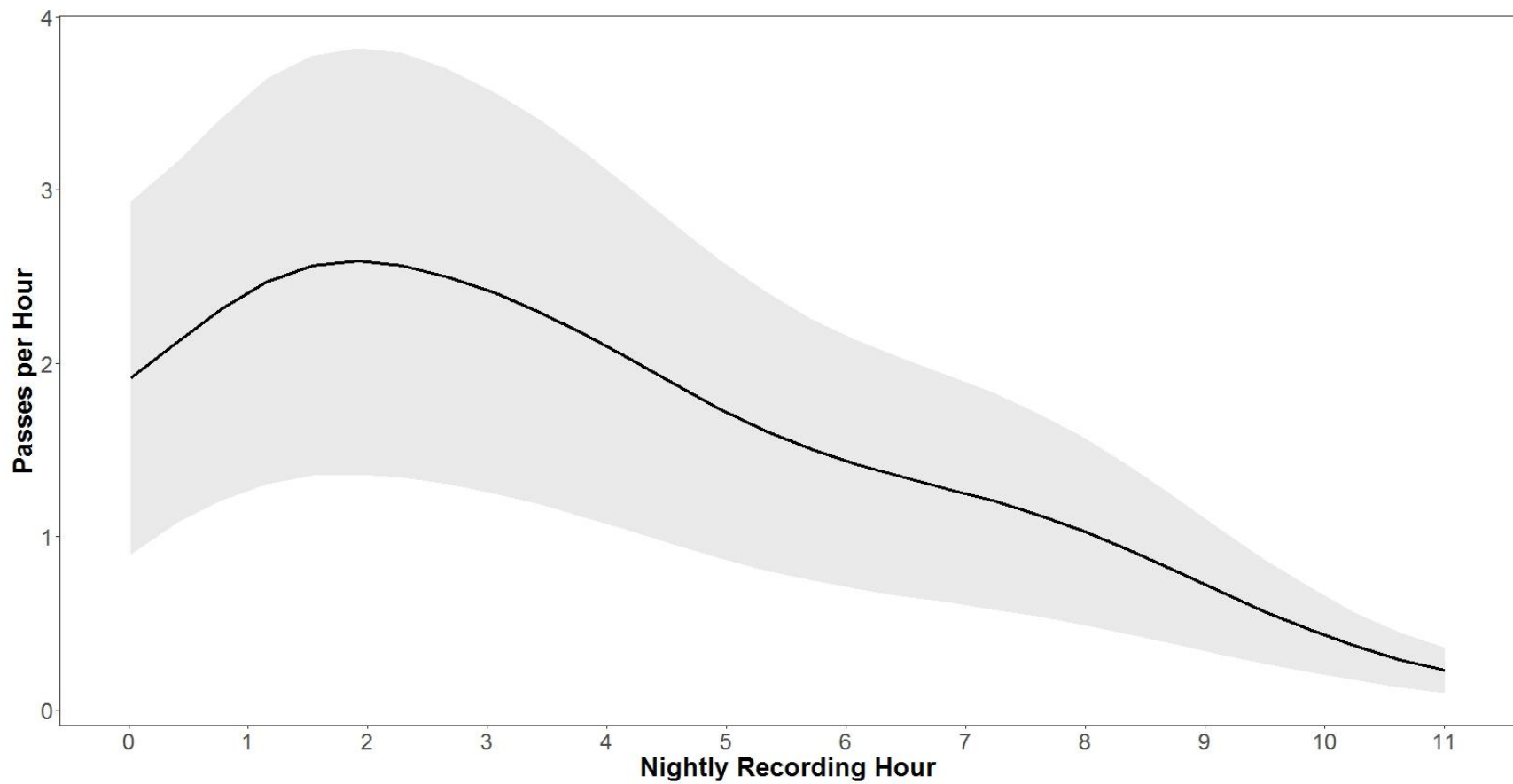
Figure 2-42: Partial effects plot of the relationship between sampling hour of night and silver-haired bat (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
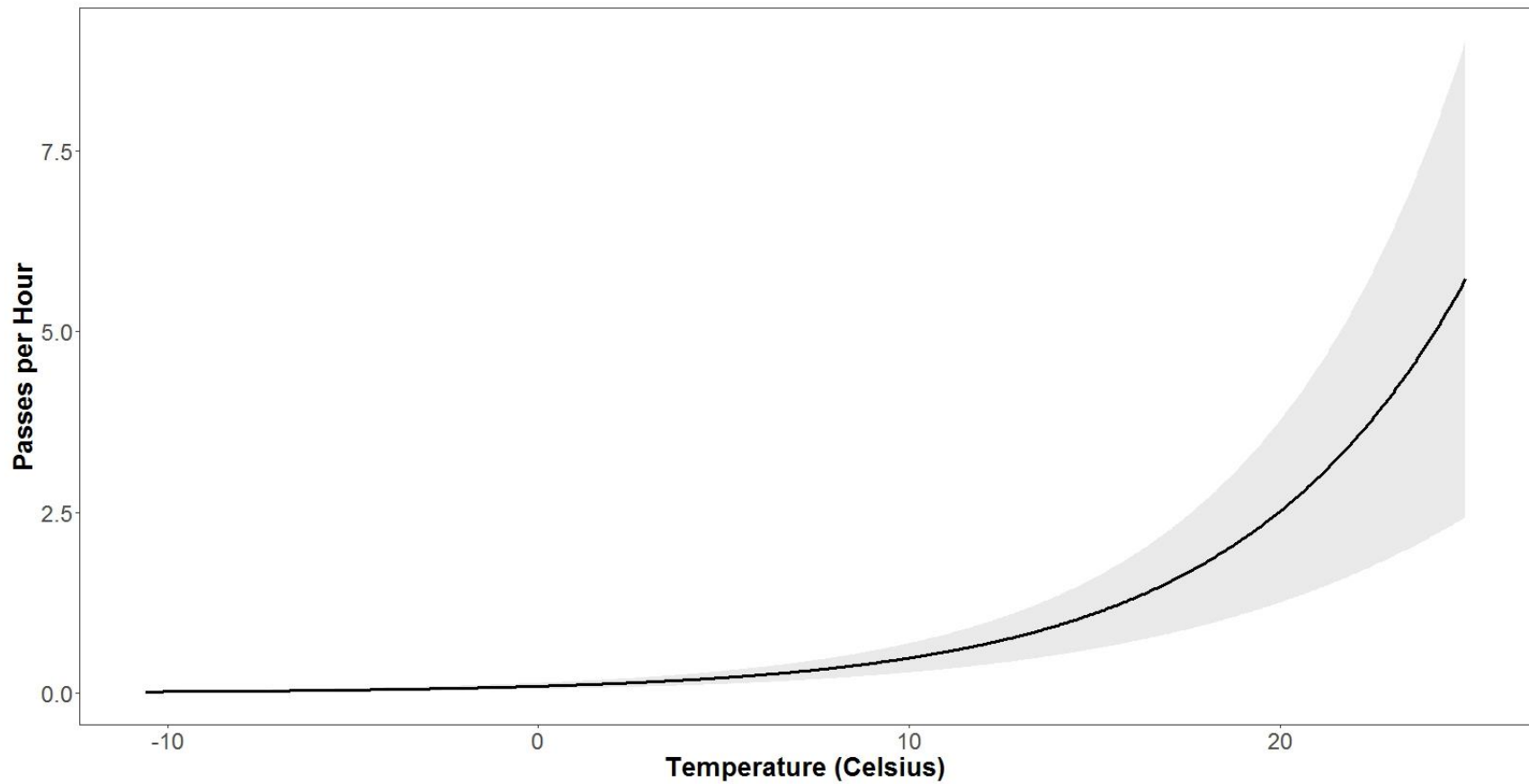
Figure 2-43: Partial effects plot of the relationship between hourly ambient temperature (Celsius) and silver-haired bat (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
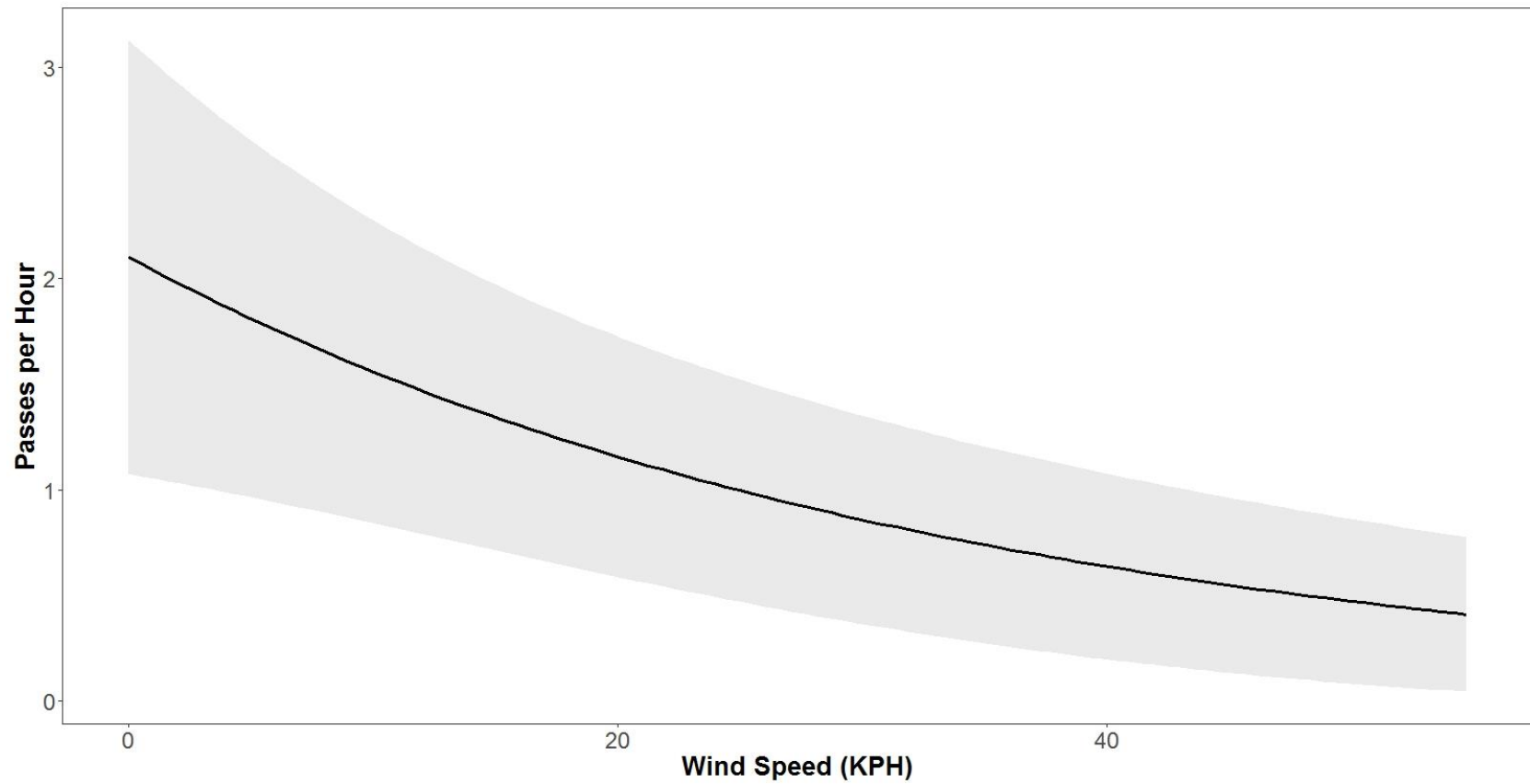
Figure 2-44: Partial effects plot of the relationship between hourly wind speed (KPH) and silver-haired bat (*Lasionycteris noctivagans*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2015 and 2016.
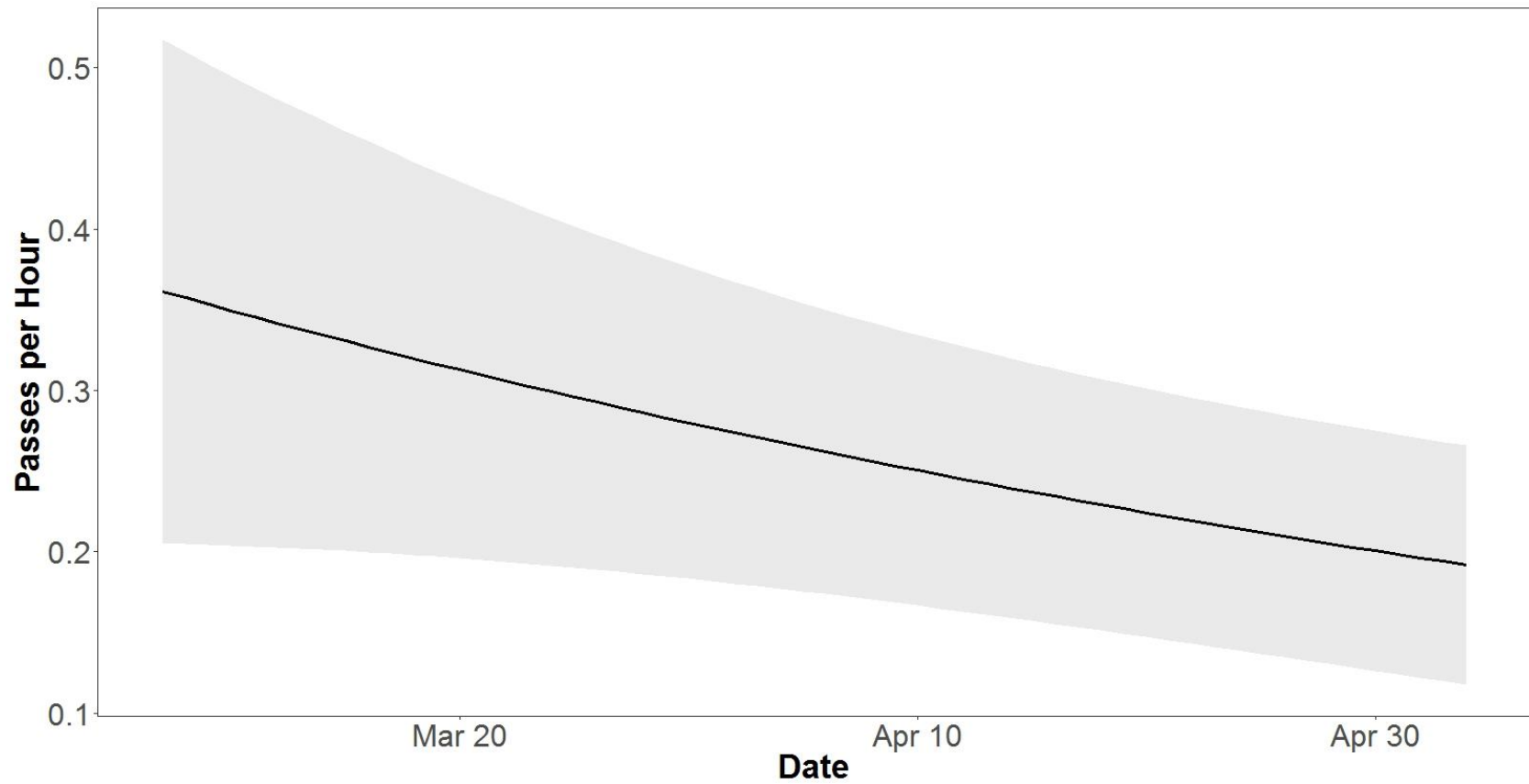
Figure 2-45: Partial effects plot of the relationship between date and eastern red bat (*Lasiurus borealis*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
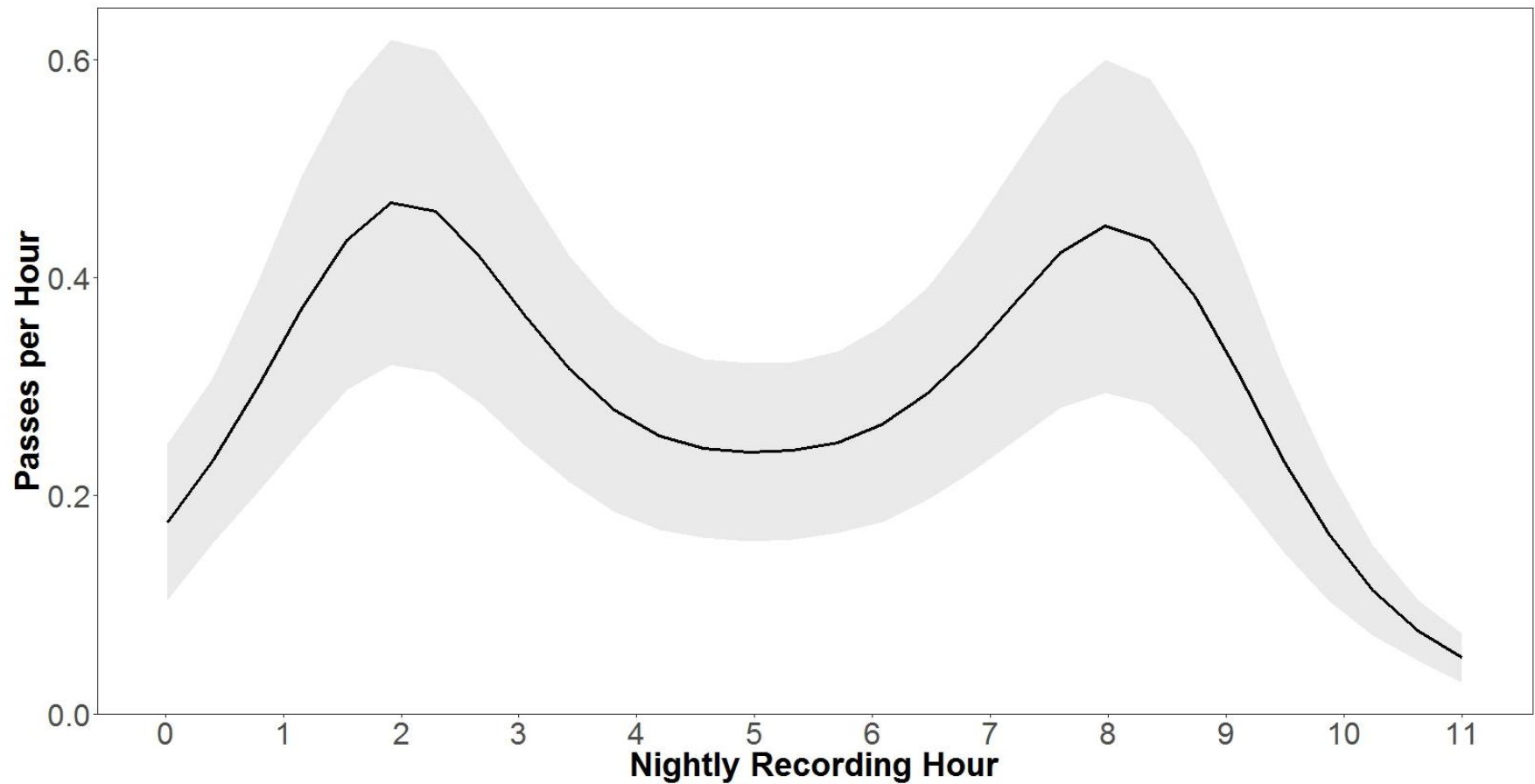
Figure 2-46: Partial effects plot of the relationship between sampling hour of night and eastern red bat (*Lasiurus borealis*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
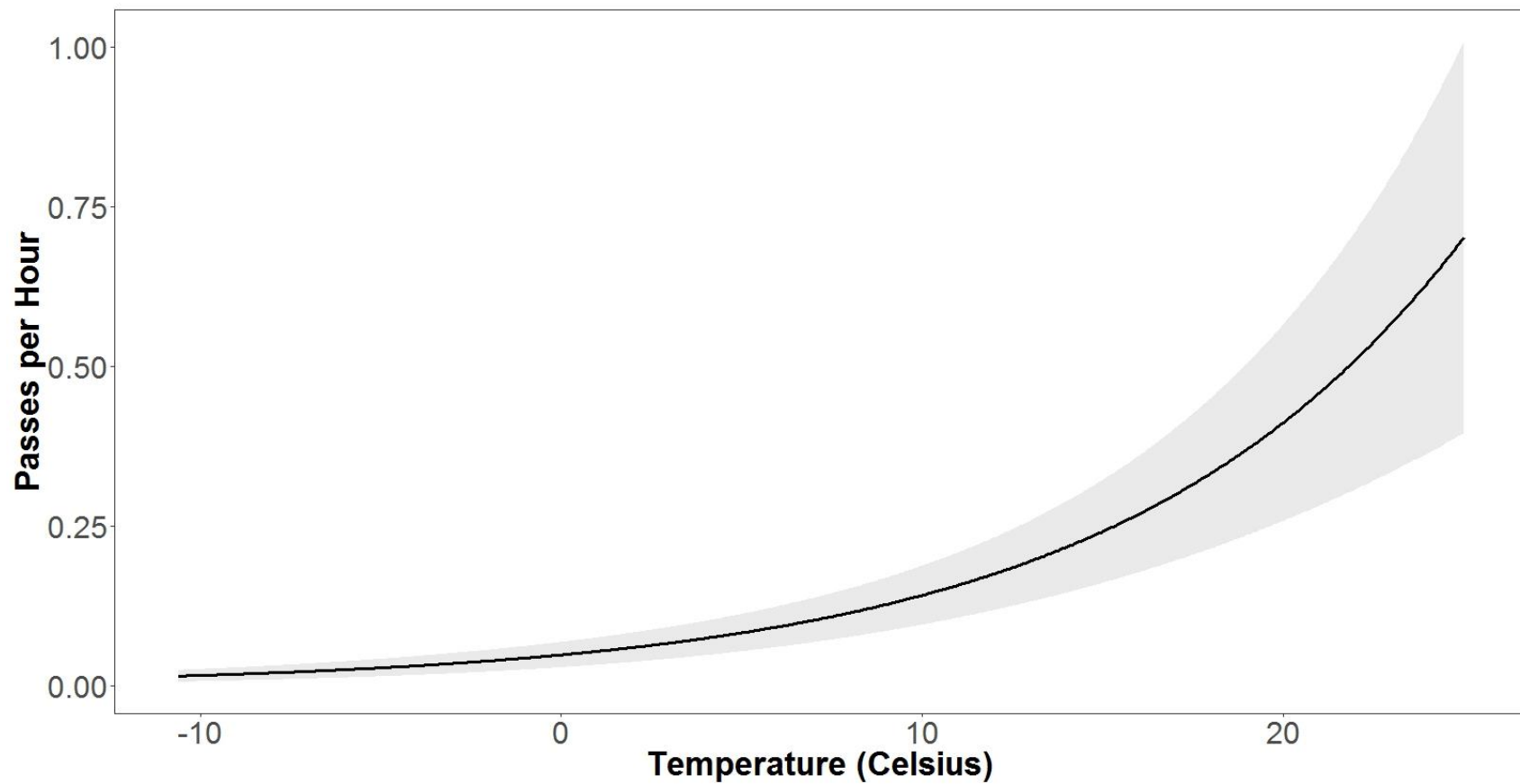
Figure 2-47: Partial effects plot of the relationship between hourly ambient temperature (Celsius) and eastern red bat (*Lasiurus borealis*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
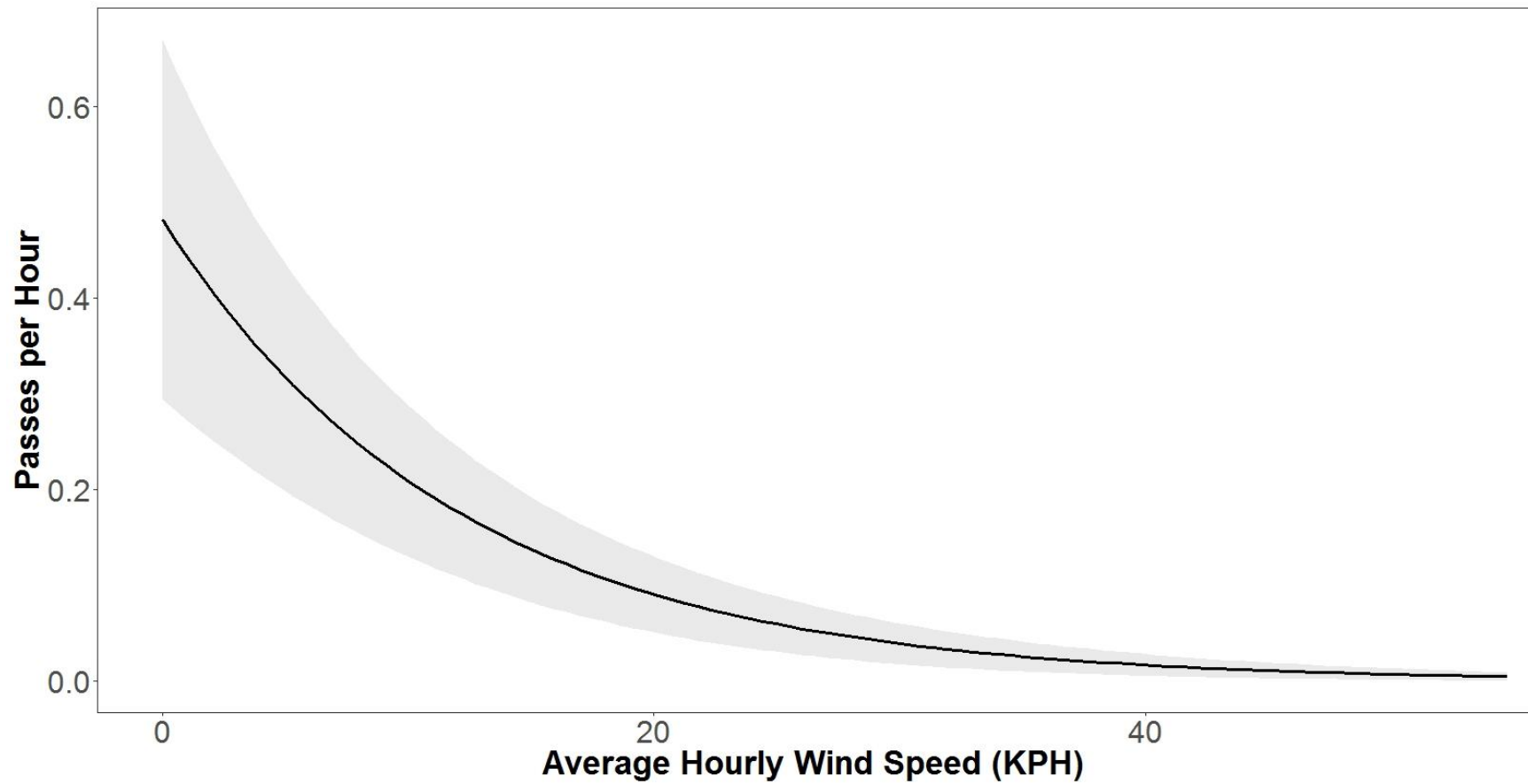
Figure 2-48: Partial effects plot of the relationship between hourly wind speed (KPH) and eastern red bat (*Lasiurus borealis*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
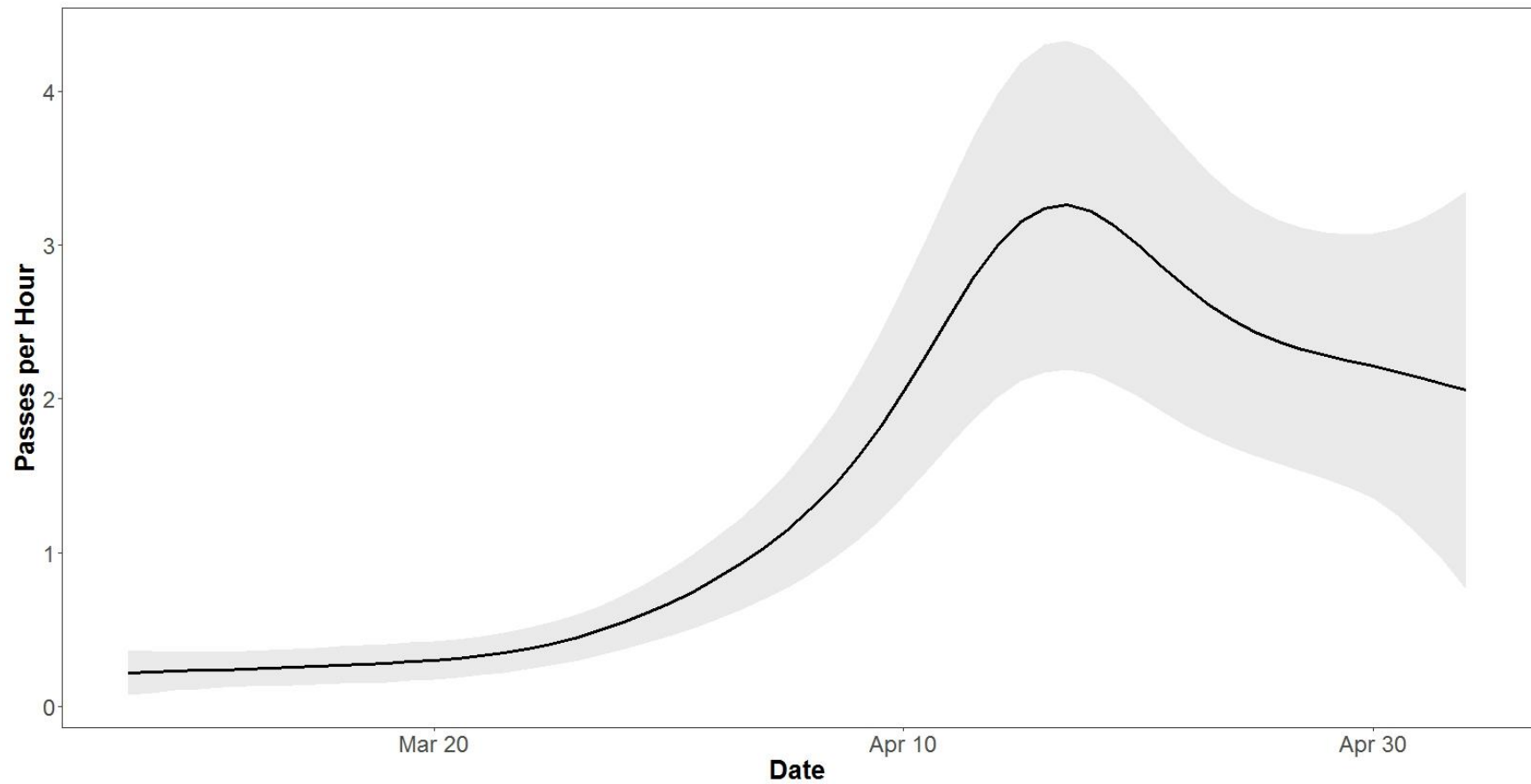
Figure 2-49: Partial effects plot of the relationship between date and hoary bat (*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
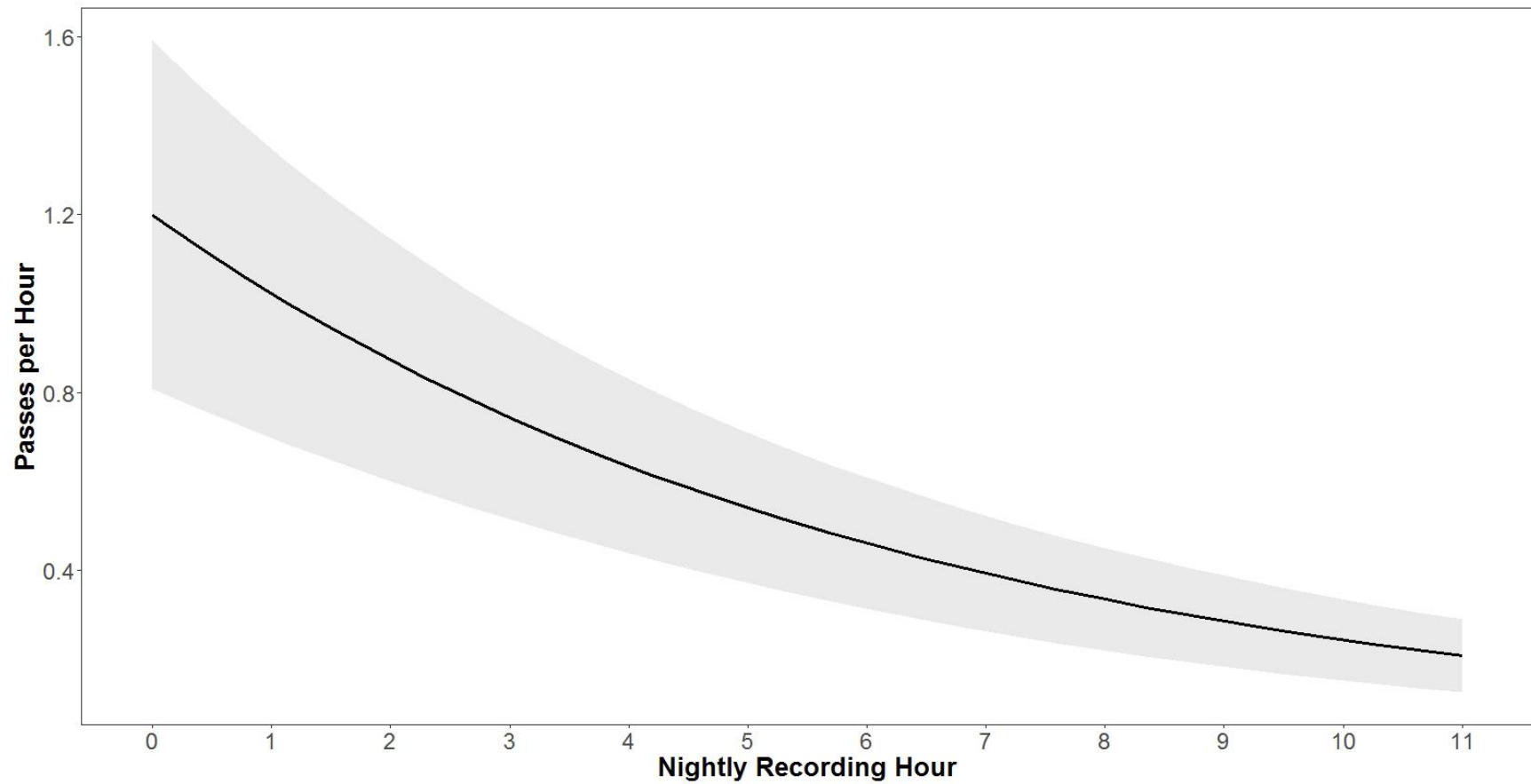
Figure 2-50: Partial effects plot of the relationship between sampling hour of night and hoary bat (*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.
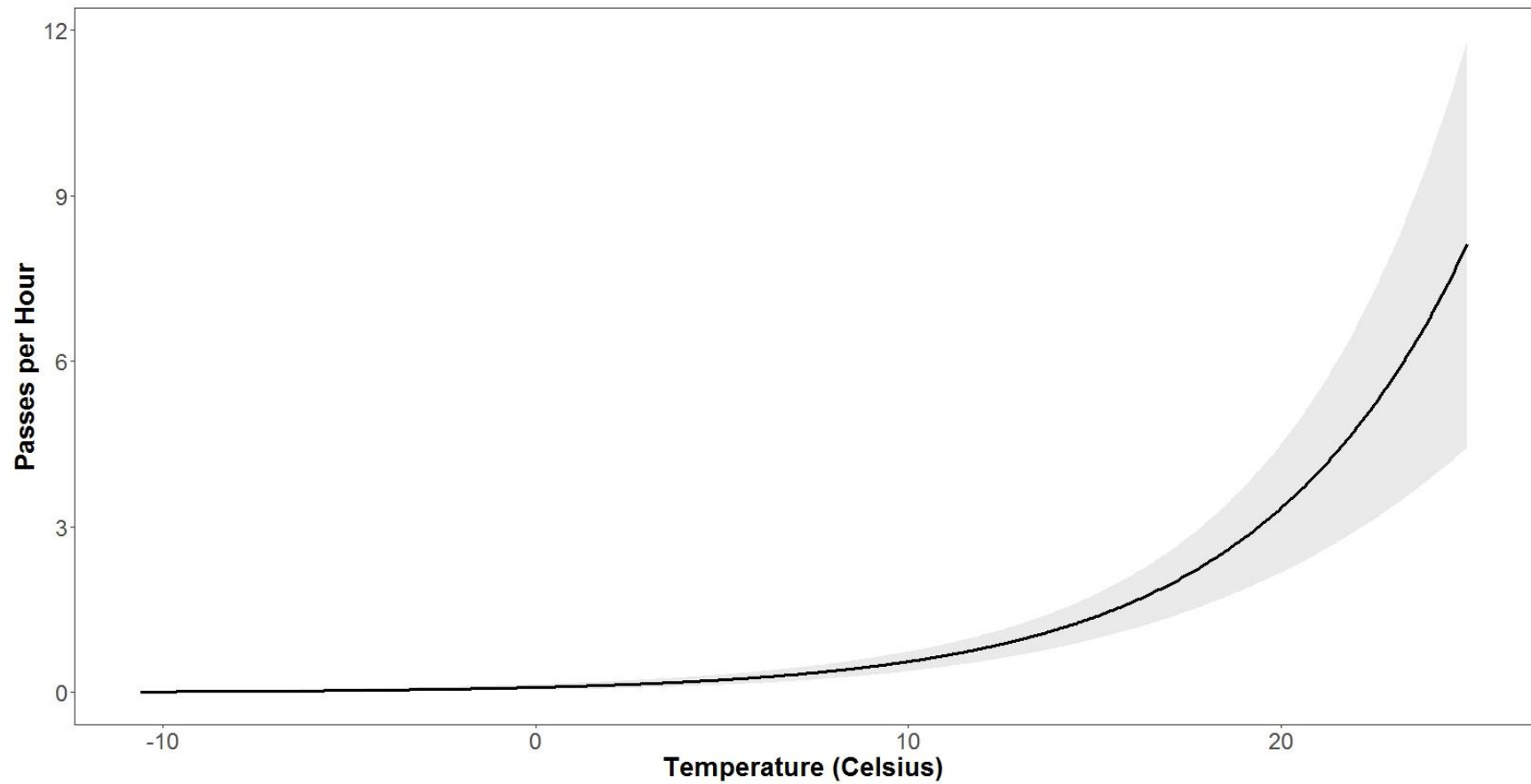
Figure 2-51: Partial effects plot of the relationship between hourly ambient temperature (Celsius) and hoary bat (*Lasiurus cinereus*) echolocation passes per hour (with 95% confidence intervals shade gray) along five ridgelines in the central Appalachians, Virginia, during spring 2016 and 2017.

Figure 2-52: Photograph of an eastern red bat (*Lasiurus borealis*) roosting in litter (left), and approximate location of roost on hillside (right) at Pandapas Pond Recreational area, George Washington and Jefferson National Forest, Montgomery County, VA, on 03/08/2015. Photograph credit: Andrew Kniowski.

*Chapter 3: Impacts of White-nose Syndrome on maternity colony day roost selection by Myotis septentrionalis in the central Appalachians*

*Abstract*

Most extant northern long-eared bat maternity colony day-roost data were gathered prior to the onset of White-nose Syndrome (WNS). Despite the informational need with threatened status under the Endangered Species Act, the difficulty in catching northern long-eared bats has meant that locating and describing post-WNS day-roosts to compare to pre-WNS is limited. Five years after the advent of WNS in Virginia, I captured and radio-tracked pregnant or lactating female northern long-eared bats to day-roosts in in the central Appalachians of Bath County, Virginia. I compared recorded day-roost characteristics to those recorded pre-WNS at the nearby Fernow Experimental Forest, Tucker County, West Virginia, and Westvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia within similar vegetation types and elevations. Post-WNS, I found that day-roost trees/snags exhibited smaller DBH values, total heights, and roost heights. Because I found no differences pre- verses post-WNS in canopy closure, surrounding forest basal area, and day-roost condition, I suggest northern long-eared bats post-WNS were still selecting similar day-roost types and structural conditions relative to the inherent differences that existed between the Virginia and West Virginia forests. Conversely, documented changes in some day roost characteristics (e.g., roost tree size) may not be a behavioral change; instead, these trends may be a result of reduced population sizes and smaller maternity colony sizes that did not require larger day-roosts. Moving forward, I suggest that pre-WNS day-roost data continue to be incorporated into current management plans, with the caveat that post-WNS fine-scale roost metrics, when available, be given greater weight.

*Introduction*

Prior to the onset of White-nose Syndrome (WNS), day-roosting ecology of the northern long-eared bat (*Myotis septentrionalis*, MYSE) had been reasonably well-documented (Owen et al. 2002, Perry and Thill 2007, Johnson et al. 2009, 2012, Rojas et al. 2017, Silvis et al. 2012, 2015*a*). During the summer maternity season, MYSE primarily roosted in tree/snag cavities or, to a lesser extent, exfoliating bark or human-made structures (Sasse and Pekins 1996, Caceres and Barclay 2000, Lacki and Schwierjohann 2001, Ford et al. 2006, Johnson et al. 2009, Lacki et al. 2009, Silvis et al. 2012, 2015*a*, Stein and White 2016).

Pregnant and lactating female MYSE roost separately from male conspecifics during the summer months, forming maternity colonies (Caceres and Barclay 2000, Ford et al. 2006). Northern long-eared bat maternity colonies are defined as the assemblage of females that use the same day-roosts within a single summer season (Silvis et al. 2014, Ford et al. 2016*a*). Historic (prior to WNS) emergence count data in the central Appalachians indicated that colonies could be quite large, > 70 individuals (Owen et al. 2002, Rojas et al. 2017), but generally were smaller groups. For example, immediately prior to WNS, Johnson et al. (2011) observed a mean of 27.2± 9.1 individuals per colony in West Virginia. Larger maternity colony size may be associated with improved social structure and colony dynamics (Ford et al. 2016*a*), but the effects of colony size on roost selection and productivity of maternity colonies largely remains unknown. Also, prior to WNS, MYSE maternity colonies characteristically were comprised of closely-related individuals, and displayed inter-annual site fidelity (Perry 2011, Patriquin et al. 2013, Silvis et al. 2015*b*). These biological traits may influence colony sizes/dynamics that have subsequently been impacted by overall population declines (Francl et al. 2012, Reynolds et al. 2016, USFWS 2017).

A single maternity colony normally uses multiple roost sites within a definable forest patch, frequently switching roosts in a non-random assorting intra-colony network dynamic (Caceres and Barclay 2000, Johnson et al. 2009, Silvis et al. 2014, Patriquin et al. 2016, Silvis et al. 2016*a*). A wide variety of tree species are used, including oaks (*Quercus* spp.), hickories (*Carya* spp.), black locust (*Robinia pseudoacacia*), sassafras (*Sassafras albidum*), and maples (*Acer* spp.). Throughout the central Appalachians and to the immediate west in the Ohio River Valley, bats strongly selected black locust and sassafras in previous studies, Lacki and Schwierjohann 2001, Ford et al. 2006, , Johnson et al. 2009, Lacki et al. 2009, Silvis et al. 2012, 2014). These tree species provide longer-lasting roost sites as either live trees or snags compared to other species with faster decay rates (Sasse and Pekins 1996, Lacki and Schwierjohann 2001, Ford et al. 2006, Johnson et al. 2009, Lacki et al. 2009, Silvis et al. 2014). Indeed, most documented day-roosts trees used by MYSE in the central Appalachians are declining live trees or snags with cavities (Owen et al. 2002, Ford et al. 2006, Johnson et al. 2009, Ford et al. 2016*a*). Tree selection is related to the characteristics of individual roost trees and the surrounding forest stand (Cryan et al. 2001, Menzel et al. 2002*b*, Carter and Feldhamer 2005, Johnson et al. 2009).

Prior to WNS, research from the northern part of MYSE range in Canada and New England or at the higher elevations encountered in the central Appalachians has shown that maternity colonies select summer day-roost sites for thermoregulatory benefits (warmth) during fetal development, lactation, and juvenile development (Garroway and Broders 2008, Henderson and Broders 2008, Patriquin et al. 2016). Less canopy closure and slope aspects that increased solar exposure and radiation were generally regarded as important characteristics of day-roosts (Desta et al. 2004, Boyles 2007, Johnson et al. 2009, Silvis 2014). Conversely, where

temperature minimums and solar exposure were not considered a limiting factor, day-roost selection may not follow these patterns (Silvis et al. 2012, Patriquin et al. 2016). A commonality from pre-WNS day-roost research, at least in the central Appalachians and Ohio River Valley, has been that in most forest types and management regimes, day-roost availability has not been a restrictive component of MYSE ecology (Menzel et al. 2002*b*, Owen et al. 2002, Ford et al. 2006, Lacki et al. 2009, Silvis et al. 2012, Ford et al. 2016*a*).

Populations of MYSE have declined precipitously due to WNS (Frick et al. 2016, Reynolds et al. 2016), creating an imperative for wildlife managers to recognize how MYSE maternity roosting ecology may be changing through this mortality event. Population declines have been so severe (> 90% mortality), the species was determined to be federally-threatened by the U.S. Fish and Wildlife Service (Department of the Interior 2015). Due to the current scarcity of MYSE across the landscape, post-WNS study of maternity colony roosting ecology is extremely challenging, leaving the effects of WNS on MYSE maternity colony roosting ecology largely unknown. If roosting ecology of MYSE maternity colonies changes concurrently with population numbers, using pre-WNS findings to guide management of roost resources may fail to avoid activities that negatively affect this threatened species (Langwig et al. 2012), or provide inadequate direction for forest management to provide day-roosting habitat to facilitate recovery (Silvis et al. 2016*b*). It is possible that MYSE will become a primary regulatory driver of upland forest management in much of the eastern United States if up-listed under the Endangered Species Act as declines continue, as they are forest habitat generalists in terms of their day-roosting and foraging habitat use (Ford et al. 2016b). Accordingly, managers need updated day-roost information that reflects post-WNS roosting ecology.

My priority objective was to determine if differences existed between pre- and post-WNS MYSE maternity colony roost selection ecology in the central Appalachians. Due to severe regional WNS-related population declines, I clearly expected that located maternity colonies would be comprised of fewer individuals than those pre-WNS colonies in the central Appalachians (Johnson et al. 2009, Silvis et al. 2012). Regardless of colony size, I expected day-roost ecology generally would be similar to pre-WNS findings, and roost selection differences would be minimal.

*Methods*

*Study Area*

My study was conducted on the George Washington and Jefferson National Forest and to a lesser extent, on adjacent private lands, in Bath County, Virginia. The forests of this area are relatively xeric-to moderately mesic oak (*Quercus* spp.) and montane pine (*Pinus* spp.) associations dominated by chestnut oak (*Quercus montana*), white oak (*Quercus alba*), Virginia pine (*Pinus virginiana*), and pitch pine (*Pinus rigida*; Braun 1950). In lower elevations and along riparian corridors, more mesic species such as white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and red maple (*Acer rubrum*) predominate. It is widely accepted that pre-European settlement, this region was comprised of more xeric oak-pine savannas with mesic hemlock-white pine mixed forest restricted to riparian areas (Nowacki and Abrams 2008, Arthur et al. 2012). Fire suppression policies starting in the early 1900s drastically changed forest composition and structure, increasing the abundance of fire-intolerant species such as red maple, American beech (*Fagus grandifolia*), blackgum (*Nyssa sylvatica*), and tulip poplar (*Liriodendron tulipifera*). Burning resumed as a restoration tool in the past few decades (Abrams 1992, Brose et

al. 2001, Arthur et al. 2012). White-nose Syndrome was confirmed to have reached hibernacula in Bath County, Virginia, in February 2009 (Reynolds et al. 2016).

For comparison to post-WNS MYSE maternity colony day-roosts, I used pre-WNS MYSE maternity colony day-roost data, 2007-2008, from the Fernow Experimental Forest (FEF) in Tucker County, West Virginia (Johnson et al. 2009). This site was on the Allegheny Plateau 100 km to the northwest of Bath County in a largely similar forest system and management regime, though slightly more mesic with a larger proportion of mesic, cove hardwood associations (Johnson et al. 2009). For a more detailed description, see Johnson et al. (2009).

*Data Collection*

I captured MYSE using mist nets (38mm mesh, reduced bag, Avinet, Portland, ME) set up over small first-order stream corridors, ephemeral pools, and single-lane forest roads from late May to late July in 2015 and 2016. I recorded age (through epiphyseal-diaphyseal fusion estimation; Anthony 1988), mass, right forearm length, sex, and reproductive condition for each bat captured (Menzel et al. 2002*a*). I affixed radio transmitters (LB-2, 0.47 g, Holohil Systems Ltd. Woodlawn, ON, Canada) to captured pregnant or lactating female bats, between the scapulae, using Perma-Type surgical cement (Perma-Type Company Inc., Plainville, CT). I put uniquely-numbered wing bands (2.4mm, Porzana Limited, Icklesham, East Sussex, U.K.) on the forearms of captured bats to identify recaptured individuals (Silvis et al. 2012). I used radio telemetry to track bats during daylight hours to locate day-roosts (Wildlife Materials TRX-1000 receivers and 3-element yagi antennae, Murphysboro, IL; Johnson et al. 2009). To capture additional members of putative maternity colonies, I surrounded located day-roosts with mist nets following the methods of Silvis et al. (2014). I expected to detect the majority of individuals within a maternity colony through tracking and capture or day-roost exit counts (Silvis et al.

2015*b*). Additionally, I performed nightly exit counts on day-roost trees that were not conducive to mist net capture. I attached radio-transmitters to all female bats captured in the netted colony, and tracked bats daily to locate additional day-roosts. In the event of a bat losing a transmitter prior to recapture, I reattached a new transmitter. I tracked bats to day-roosts until the transmitter batteries expired or until they fell off the bats.

Following the methods of Johnson et al. (2009), I measured the following tree characteristics of each day-roost tree found: locations (Garmin Rino GPS units, Olathe, KS), tree species, diameter at breast height (dbh tape, Forestry Suppliers Inc., Jackson, MS), decay stage, crown class, tree height (using a clinometer, Brunton, Louisville, CO), roost type where observable, and roost height where observable. I visually estimated the percentage of bark on each roost tree. I categorized decay stage of each roost tree using numbers corresponding to a qualitative value: 1 = live, 2 = declining, 3 = recent dead, 4 = loose bark, 5 = no bark, 6 = broken top, 7 = broken bole (Cline et al. 1980). I categorized crown class using a similar scheme: 1 = suppressed, 2 = intermediate, 3 = codominant, 4 = dominant (Nyland 2002). I recorded similar characteristics for the four trees nearest the roost tree using the point-centered quarter method and measured their distances to each roost tree (Mitchell 2010). I used a concave densitometer (Forestry Suppliers Inc., Jackson, MS) to record canopy closure and a 20-factor prism (JIM-GEM®, Jackson, MS) to measure the basal area around each roost tree.

I used ArcMap 10.3.1® software (ESRI, Redlands, CA) to generate 2 random points for each roost tree found in the summer of 2015 and 2016. I placed half of these random points within a minimum convex polygon of the roost trees from each maternity colony, and the remaining random points were within a buffer around the minimum convex polygon. I located

these random points in the field using GPS, and chose the closest tree for random tree measurement. I measured the same variables at random trees as day-roosts.

*Statistical Analyses*

To measure differences in tree metrics between pre-WNS and post-WNS roost trees and between post-WNS roost trees and random trees, I used two-sample Wilcoxon tests for simple comparisons of continuous measures, similar to the protocol of Silvis et al. (2012). Due to small sample sizes, I pooled roost tree data from summer 2015 and 2016. I used Fisher's Exact Tests (FET) to determine equitability of the distribution of categorical variables between pre and post-WNS roost trees and between post-WNS roost trees and random trees. For all statistical analyses, I used the R statistical program, version 3.2.3 (R. Development Core Team 2014). I established significance for all tests at $\alpha \leq 0.05$.

## Results

Between May 20 and July 31 in 2015, and between May 23 and July 29 in 2016, I captured and affixed transmitters to three female MYSE (three pregnant but zero lactating upon initial capture) in 2015 and seven (one pregnant and six lactating upon initial capture) in 2016, respectively. Day-roost exit counts at single roost trees ranged from zero (visited tree known to have bats on prior occasions) to five bats in 2015 (mean = 1.73, SD = 2.1, and from zero to seven in 2016 (mean = 1.43, SD = 2.57. I considered maternity colonies from each year to be distinct colonies, although each group of day-roosts was in close proximity on the landscape (Figure 3-53). I did not capture juvenile bats in either year, and each colony from 2015 and 2016 appeared to disaggregate by June 12 and June 10, respectively. I continued netting and tracking efforts within the initial roosting areas in 2015 and 2016, but was unsuccessful in catching additional MYSE or recapturing previously-caught MYSE.

I located six day-roosts in 2015 and nine day-roosts in 2016, representing three and six tree species, respectively, for a total of six tree species observed (Tables

Table 3-*34* The tree species used as day-roosts post-WNS were significantly different (number of species and proportion of use) than the species used pre-WNS (Table 3-35, $P = 0.006$, FET). Additionally, fewer tree species were used as day-roosts post-WNS compared to tree species available on the landscape (Table 3-35, $P = 0.009$, FET).

Of the 15 day-roosts that I observed over the duration of the study, 11 of 15 were snags, a similar proportion as those located pre-WNS (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
|---|---|---|
| *N* | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of *N*) | 73.3* | 33.3* |
| Dominant crown class (% of *N*) | 40.0* | 26.7 |
| Codominant crown class (% of *N*) | 20.0* | 16.7 |
| Intermediate crown class (% of *N*) | 40.0* | 43.3 |
| Suppressed crown class (% of *N*) | 0.0* | 13.3 |

Table 3-*37*, *P* = 0.49, FET). Furthermore, day-roosts located post-WNS were in snags more than

expected based on availability in the surrounding forest stands (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

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Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
|---|---|---|
| $N$ | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of $N$) | 73.3* | 33.3* |
| Dominant crown class (% of $N$) | 40.0* | 26.7 |
| Codominant crown class (% of $N$) | 20.0* | 16.7 |
| Intermediate crown class (% of $N$) | 40.0* | 43.3 |
| Suppressed crown class (% of $N$) | 0.0* | 13.3 |

Table 3-*37*, *P* = 0.025, FET). Thirteen day-roosts found post-WNS were cavity roosts whereas

two were exfoliating bark roosts, analogous to day-roosts found pre-WNS (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
|---|---|---|
| N | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of N) | 73.3* | 33.3* |
| Dominant crown class (% of N) | 40.0* | 26.7 |
| Codominant crown class (% of N) | 20.0* | 16.7 |
| Intermediate crown class (% of N) | 40.0* | 43.3 |
| Suppressed crown class (% of N) | 0.0* | 13.3 |

Table 3-*37*, *P* = 1, FET). However, day-roost trees, located post-WNS, were significantly shorter than day-roost trees located pre-WNS (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
| --- | --- | --- |
| N | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of N) | 73.3* | 33.3* |
| Dominant crown class (% of N) | 40.0* | 26.7 |
| Codominant crown class (% of N) | 20.0* | 16.7 |
| Intermediate crown class (% of N) | 40.0* | 43.3 |
| Suppressed crown class (% of N) | 0.0* | 13.3 |

Table 3-*37*, W = 757, *P* = 0.005), but similar to randomly selected trees (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
|---|---|---|
| *N* | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of *N*) | 73.3* | 33.3* |
| Dominant crown class (% of *N*) | 40.0* | 26.7 |
| Codominant crown class (% of *N*) | 20.0* | 16.7 |
| Intermediate crown class (% of *N*) | 40.0* | 43.3 |
| Suppressed crown class (% of *N*) | 0.0* | 13.3 |

Table 3-*37*, W = 262, *P* = 0.38). Roost heights in day-roosts found post-WNS were significantly

lower than roost heights in day-roosts found pre-WNS (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
|---|---|---|
| $N$ | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of $N$) | 73.3* | 33.3* |
| Dominant crown class (% of $N$) | 40.0* | 26.7 |
| Codominant crown class (% of $N$) | 20.0* | 16.7 |
| Intermediate crown class (% of $N$) | 40.0* | 43.3 |
| Suppressed crown class (% of $N$) | 0.0* | 13.3 |

Table 3-*37*, W = 592, *P* = 0.008). Average dbh of post-WNS day-roosts was significantly less

than that of pre-WNS day-roosts (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
|---|---|---|
| *N* | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of *N*) | 73.3* | 33.3* |
| Dominant crown class (% of *N*) | 40.0* | 26.7 |
| Codominant crown class (% of *N*) | 20.0* | 16.7 |
| Intermediate crown class (% of *N*) | 40.0* | 43.3 |
| Suppressed crown class (% of *N*) | 0.0* | 13.3 |

Table 3-*37*, W = 795, *P* = 0.001), yet similar to randomly selected trees (

Table 3-*35*: Tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (Myotis septentrionalis) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
| --- | --- | --- |
| $N$ | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of $N$) | 73.3* | 33.3* |
| Dominant crown class (% of $N$) | 40.0* | 26.7 |
| Codominant crown class (% of $N$) | 20.0* | 16.7 |
| Intermediate crown class (% of $N$) | 40.0* | 43.3 |
| Suppressed crown class (% of $N$) | 0.0* | 13.3 |

Table 3-*37*, W = 215.5, *P* = 0.83). Percentage of bark remaining on the bole was similar between day-roost found post-WNS and those found pre-WNS (Table 3-2, W = 416, *P* = 0.24), but day-roosts located post-WNS had significantly less bark remaining compared to randomly-selected trees (Table 3-2, W = 329.5, *P* = 0.006).

The forest stand basal area surrounding day-roosts located post-WNS was similar to stands surrounding day-roosts located pre-WNS and similar to randomly selected trees (Table 3-2, W = 550, *P* = 0.71, W = 193.5, *P* = 0.45, respectively). Day-roosts located post-WNS had significantly greater percent canopy closure than day-roosts located pre-WNS (Table 3-2, W = 322, *P* = 0.02), but canopy closure was similar to randomly selected trees (Table 3-2, W = 278, *P* = 0.21). Finally, 46.7% of day roosts located post-WNS were located on slopes with southern aspects, significantly fewer than the 81.2% of day roosts located pre-WNS (

|  | Post-WNS day roosts | Random Trees |
|---|---|---|
| *N* | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of *N*) | 73.3* | 33.3* |
| Dominant crown class (% of *N*) | 40.0* | 26.7 |
| Codominant crown class (% of *N*) | 20.0* | 16.7 |
| Intermediate crown class (% of *N*) | 40.0* | 43.3 |
| Suppressed crown class (% of *N*) | 0.0* | 13.3 |

**Table 3-37***Tables*

Table 3-*34*, *P* = 0.009, FET), but a similar percentage compared to 50.0% of randomly selected trees (Table 2, *P* = 1, FET). Finally,

46.7% of day roosts located post-WNS were located on slopes with southern aspects, significantly fewer than the 81.2% of day roosts

located pre-WNS (

| | Post-WNS day roosts | Random Trees |
|---|---|---|
| *N* | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of *N*) | 73.3* | 33.3* |
| Dominant crown class (% of *N*) | 40.0* | 26.7 |
| Codominant crown class (% of *N*) | 20.0* | 16.7 |
| Intermediate crown class (% of *N*) | 40.0* | 43.3 |
| Suppressed crown class (% of *N*) | 0.0* | 13.3 |

**Table 3-37***Tables*

Table 3-*34*, *P* = 0.009, FET), but a similar percentage compared to 50.0% of randomly selected

trees (Table 2, *P* = 1, FET).


*Discussion*

Results suggest that many of the characteristics of MYSE maternity colony day-roosts

remain unchanged, whereas others differed either post-WNS or due to the variation in forest

conditions between Bath County (Virginia) and the Fernow Experimental Forest (Tucker

County, West Virginia). The proportion of snags and cavity-roosts used, and amount of bark

remaining on day-roosts used was similar between maternity colonies located pre- and post-

WNS. Research prior to WNS in the central Appalachians near this study site showed that cavity

roosts are common amongst MYSE maternity colonies, offering protection, thermal benefits, and

are readily available in upland deciduous forests (Menzel et al. 2002*b*, Owen et al. 2002, Johnson

et al. 2009, Silvis 2014, Silvis et al. 2015*a*). Furthermore, snags are more likely to have cavities

than live trees, and the amount of bark remaining on bole is correlated with mortality condition

(Goodburn and Lorimer 1998, Fan et al. 2003, Eskelson et al. 2009). Results indicate that WNS

likely has not changed this integral part of MYSE maternity colony day-roosting ecology.

Perhaps most surprising were the significantly smaller diameters of day-roosts used by

post-WNS MYSE maternity colonies, compared to day-roosts used in pre-WNS surveys

(Johnson et al. 2009). Because the MYSE maternity colonies that I located were comprised of

only a few individuals, perhaps smaller diameter day-roosts offered greater thermoregulatory and

social benefits, as cavity volume is likely to be lower and fewer bats are required to fill overall

roost space. This could potentially reduce energetic costs associated with maintaining high body

temperatures (Hamilton and Barclay 1994, Willis et al. 2006, Garroway and Broders 2008, Henderson and Broders 2008). Still, the effects of internal cavity size and characteristics on roost selection ecology and reproductive behaviors of MYSE maternity colonies in a post-WNS environment merits further study (Silvis et al. 2015*c*).

If small maternity colonies select day-roosts for increased/shared warmth due to fuller cavities, I would also expect roosts to be located in places with a higher degree of solar radiation for even greater roost warmth (Kerth et al. 2001, Lourenço and Palmeirim 2004, Boyles 2007, Silvis et al. 2015*a*). However, I found no differences in canopy closure between day-roosts used by maternity colonies post-WNS and randomly-selected trees. These data suggest that bats may have selected for day-roosts based on criteria other than canopy closure, and/or there was less availability of potential roost trees with smaller diameters and greater canopy openness on the landscape. Similarly, I expected the majority of roost locations to be on warmer, southerly aspects (Desta et al. 2004). However, available aspects are partly controlled to the orientation of the overall linear ridges locally. Thus, day-roosts selected post-WNS appear to have been located on the warmest areas at my study sites that did not lack availability of other roost characteristics. Canopy closure and other microclimate characteristics such as slope and aspect may not be as important as tree dbh/cavity size for maternity colony roost selection, especially for smaller colonies. Indeed, social thermoregulation is more important than microclimate characteristics at roost sites for big brown bat (*Eptesicus fuscus*) energy balance, and this may be the case for MYSE maternity colonies as well (Willis and Brigham 2007).

If pregnancies are not viable or pups die before volancy, physiological constraints for MYSE females may be relaxed. Non-reproductive females may be able to enter torpor regularly, and thus may select day-roosts with characteristics other than warmth (unlikely behavior in

pregnant bats; Hamilton and Barclay 1994; Willis et al. 2006). Pettit and O'Keefe (2017) observed big brown bats that lost pups due to effects of WNS, and this may be occurring in MYSE maternity colonies as well. Though each female captured in 2015 and 2016 showed some evidence of reproductive characteristics (i.e. pregnant and lactating), no juvenile bats were captured and all individuals appeared to leave the landscape prior to when juveniles would have become volant (Johnson et al. 2013). It is possible that both maternity colonies I initially located in 2015 and 2016 moved as a social group to an entirely new geographic area where I could not detect them. However, such colony-wide movement pre-volancy is unlikely (Silvis et al. 2014). It also is possible that maternity colonies in 2015 and 2016 failed to successfully produce offspring, corroborating prior research assessing population-scale impacts of WNS on MYSE (Francl et al. 2012, Reynolds et al. 2016, Pettit and O'Keefe 2017). Nonetheless,my study shows it is unlikely a major shift in day-roosting selection is occurring and thus recruitment failure likely is the cause of changes in some other aspect of MYSE ecology.

Variation observed in day-roost selection between pre- and post-WNS MYSE maternity colonies included in my study may be a product of different colony locations and the associated surrounding forests. Although the forests surrounding the pre and post-WNS colonies used in these analyses appear qualitatively similar (Braun 1950, Ford et al. 2005, Johnson et al. 2009), there may be important differences in local forest management activities, topography, geology, climate, and biotic communities which could relate to distinctly different day-roost ecology between MYSE maternity colonies. Indeed, even local variability of maternity colony roost selection has been reported, between years and within a single season across the MYSE distribution (Garroway and Broders 2007, 2008, Silvis et al. 2012, 2015*a*). Regardless, the forests are climatically and compositionally more similar than dissimilar, and offer a reasonable

starting point to determine how day-roost ecology of MYSE maternity colonies may be changing with the protraction of WNS. I assumed maternity colonies that I located in Bath County, Virginia, would have been comprised of more individuals prior to WNS-related declines, yet no data exist on maternity colony size prior to WNS on the local landscape.

Despite the extreme population declines of MYSE in the past decade, understanding how WNS impacts day-roosting ecology of MYSE maternity colonies is needed by managers trying to protect remaining populations. As my study shows, MYSE maternity colonies post-WNS may be selecting smaller trees than those selected by maternity colonies pre-WNS. However, because of my small sample size and potential habitat variation between maternity colonies located in West Virginia pre-WNS and those located in Virginia post-WNS, my comparative analyses should be interpreted with caution. At a minimum, WNS appears to affect MYSE maternity colony ecology by disrupting the reproductive cycle and reducing recruitment (Francl et al. 2012, Reynolds et al. 2016). Research on day-roost ecology of MYSE maternity colonies where WNS remains absent should continue, and researchers must be prepared to take advantage of future opportunities to study MYSE maternity colonies where WNS is already present. These data potentially will offer detailed insight into how WNS affects day-roosting ecology of MYSE maternity colonies, thus helping managers implement best management practices to conserve these threatened populations.

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*Tables*

Table 3-34: Female northern long-eared bat (*Myotis septentrionalis*) day roosts by tree species, number found, percentage of total day roosts, roost days (number of days used) by radio-tagged bats, and percentage of total roost days by radio-tagged bats in deciduous hardwood forest on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016.

| Tree Species | Day roosts | % Total day roosts | # Roost days | % Total roost days |
|---|---|---|---|---|
| Red Maple (*Acer rubrum*) | 5 | 33 | 13 | 33 |
| Chestnut oak (*Quercus montana*) | 4 | 27 | 6 | 15 |
| Sassafras (*Sassafras albidum*) | 2 | 13 | 2 | 5 |
| Blackgum (*Nyssa sylvatica*) | 2 | 13 | 14 | 35 |
| Hickory (*Carya* spp.) | 1 | 7 | 4 | 10 |
| Black locust (*Robinia pseudoacacia*) | 1 | 7 | 1 | 3 |

Table 3-35: Tree species selected as day-roosts and % total uses by female northern long-eared bat (*Myotis septentrionalis*) maternity colonies on George Washington and Jefferson National Forest and adjacent private lands in Bath County, Virginia, 2015 and 2016 (following White-nose Syndrome, Post-WNS); randomly selected trees within landscape surrounding Post-WNS day-roosts; and tree species selected as day-roosts and % total uses by female northern long-eared bat (*Myotis septentrionalis*) maternity colonies on the Fernow Experimental Forest, Tucker County, Virginia, 2007 and 2008 (prior to White-nose Syndrome, Pre-WNS).

| Tree species | Post-WNS day roosts | % Total Post-WNS day roosts | Random trees | % Total random trees | Pre-WNS day roosts | % Total Pre-WNS day roosts |
|---|---|---|---|---|---|---|
| *Acer rubrum* | 5 | 33 | 0 | 0 | 10 | 14.3 |
| *Quercus* spp. | 4 | 27 | 11 | 36.7 | 10 | 14.3 |
| *Nyssa slyvatica* | 2 | 13 | 7 | 23.3 | 0 | 0.0 |
| *Sassafras albidum* | 2 | 13 | 1 | 3.3 | 5 | 7.1 |
| *Carya* spp. | 1 | 7 | 1 | 3.3 | 1 | 1.4 |
| *Robinia pseudoacacia* | 1 | 7 | 2 | 6.7 | 34 | 48.6 |
| *Liriodendron tulipifera* | 0 | 0 | 1 | 3.3 | 1 | 1.4 |
| *Prunus serotina* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| *Magnolia* spp. | 0 | 0 | 0 | 0.0 | 1 | 1.4 |
| *Oxydendrum arboreum* | 0 | 0 | 0 | 0.0 | 3 | 4.3 |
| Unknown | 0 | 0 | 0 | 0.0 | 2 | 2.9 |
| Other | 0 | 0 | 7 | 23.3 | 0 | 0.0 |

Table 3-36: Mean ± SD values of day roost characteristics and percent of trees in each crown class for Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, VA) and randomly selected trees located within and on the surrounding landscape. An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of randomly selected trees.

|  | Post-WNS day roosts | Random Trees |
| --- | --- | --- |
| *N* | 15 | 30 |
| dbh (cm) | 16.33 ± 7.12* | 18.32 ± 12.96* |
| Tree height (m) | 10.26 ± 6.44* | 11.12 ± 6.13 |
| Canopy closure (%) | 87.99 ± 14.14* | 91.98 ± 17.59 |
| Bark remaining (%) | 60.87 ± 33.08* | 90.90 ± 20.74* |
| Surrounding basal area m²/ha | 32.75 ± 16.08* | 28.62 ± 9.00* |
| Dead/declining (% of *N*) | 73.3* | 33.3* |
| Dominant crown class (% of *N*) | 40.0* | 26.7 |
| Codominant crown class (% of *N*) | 20.0* | 16.7 |
| Intermediate crown class (% of *N*) | 40.0* | 43.3 |
| Suppressed crown class (% of *N*) | 0.0* | 13.3 |

Table 3-37: Mean ± SD values of day roost characteristics and percent of trees in each crown class for pre-White-nose Syndrome (WNS) day roost trees located on the Fernow Experimental Forest (Tucker County, West Virginia) and Post-WNS day roost trees located on George Washington and Jefferson Forest and private lands (Bath County, Virginia). An asterisk (*) indicates a significant difference ($P < 0.05$) between characteristics of day roosts located post-WNS and those of day roosts located pre-WNS.

|  | Pre-WNS day roosts | Post-WNS day roosts |
|---|---|---|
| $N$ | 69 | 15 |
| dbh (cm) | 28.53 ± 17.22* | 16.33 ± 7.12* |
| Tree height (m) | 15.45 ± 7.46* | 10.26 ± 6.44* |
| Roost height (m) | 8.69 ± 4.51* | 5.37 ± 3.64* |
| Cavity roost (% of $N$) | 84.1 | 86.7 |
| Canopy closure (%) | 80.02 ± 19.32* | 87.99 ± 14.14* |
| Bark remaining (%) | 69.40 ± 40.70 | 60.87 ± 33.08* |
| Surrounding Basal Area m²/ha | 34.20 ± 10.40 | 32.75 ± 16.08* |
| Dead/Declining (% of $N$) | 81.2 | 73.3* |
| Dominant crown class (% of $N$) | 4.4* | 40.0* |
| Codominant crown class (% of $N$) | 39.1* | 20.0* |
| Intermediate crown class (% of $N$) | 33.3* | 40.0* |
| Suppressed crown class (% of $N$) | 23.2* | 0.0* |
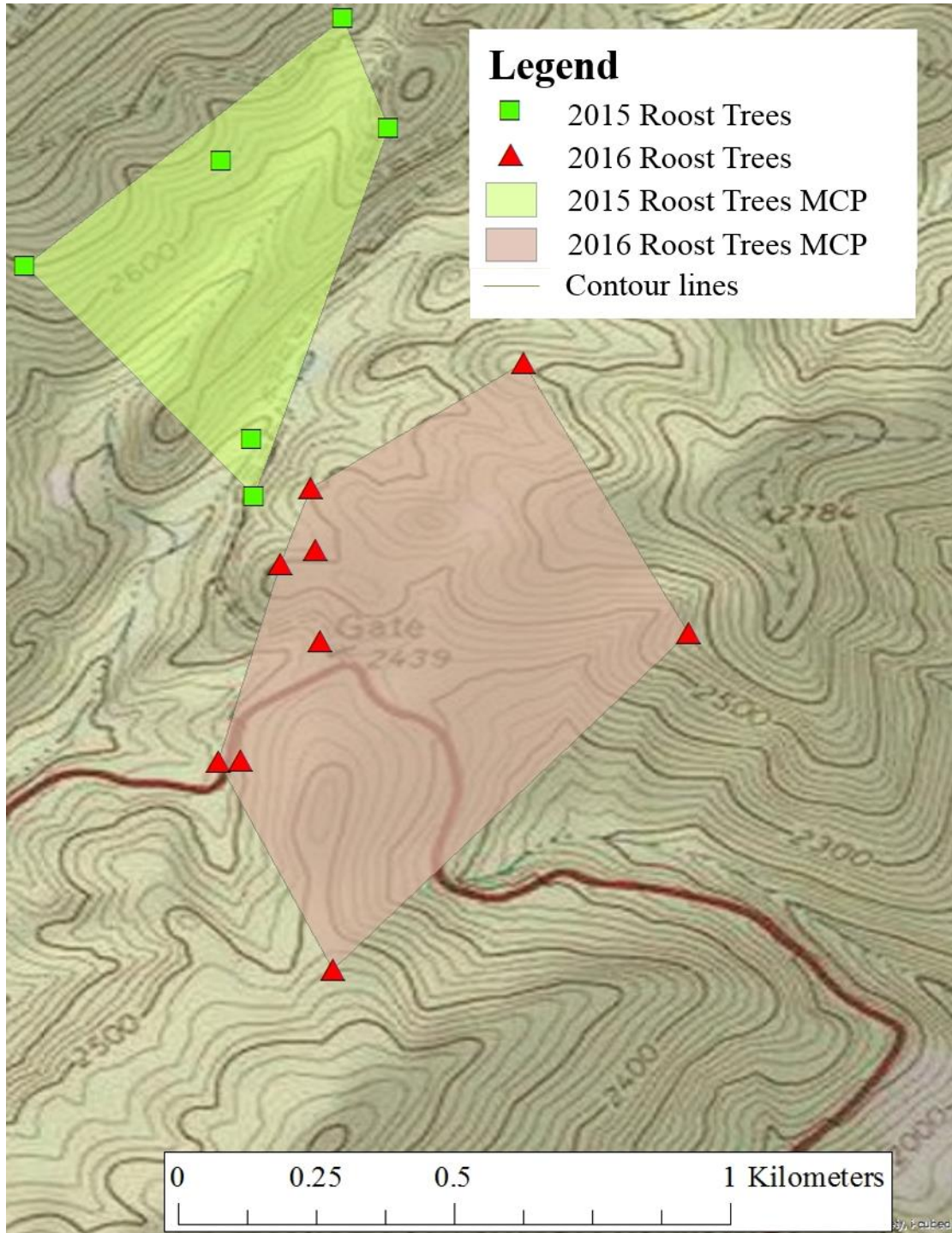
Figure 3-53: Locations of female northern long-eared bat day roosts found in Bath County, Virginia, during summer 2015 and 2016. The minimum convex polygon (MCP) for 2015 roosts encompassed 20.8 hectares, and the MCP for the 2016 roosts encompassed 39.8 hectares.